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The Status of Atlantic Salmon: Populations and Habitats

Québec, Quebec, Canada
11–14 August 2003

[Le statut du saumon atlantique: populations et habitats]

Québec, Québec, Canada
11–14 août 2003

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Daniel Boisclair
Département de sciences biologiques
Université de Montréal
Montréal, Quebec

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Faskally, Pitlochry, Perthshire, UK

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Donna L. Parrish
Vermont Cooperative Fish and Wildlife Research Unit
The Rubenstein School of Environment and Natural Resources
University of Vermont
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INTRODUCTION / INTRODUCTION

The status of Atlantic salmon (*Salmo salar*): populations and habitats

Daniel Boisclair

Abstract: The important decline of Atlantic salmon (*Salmo salar*) across its range during the past three decades, despite numerous management and conservation programmes, is an alarming index of the vulnerability of this species. The following series of papers was produced to summarize current knowledge on specific interactions between biotic and abiotic variables that may contribute to determine the survival of Atlantic salmon. Evaluation of the challenges encountered in spawning grounds (siltation, oxygenation), nursery habitats (substrate, trophic interactions), overwintering habitats (flow conditions, winter feeding opportunities), and coastal and oceanic environments (water temperature, predators, parasites) suggest that all habitats required by Atlantic salmon and all processes that occur in each habitat represent a critical link that allows this species to persist. Management practices employed during artificial fish selection, incubation, and stocking also affect the success of restoration efforts. Because limiting factors may change in time and because our ability to intervene in specific habitats may be minimal, the only strategy within our reach may be to continue gathering information about processes that determine the fragility of Atlantic salmon and, in the light of our findings, to implement scientifically sound actions where and when possible.

Résumé : L'important déclin du saumon atlantique (*Salmo salar*) sur toute son aire de distribution au cours des trois dernières décennies, malgré de nombreux programmes de gestion et de conservation, est un indice alarmant de la vulnérabilité de cette espèce. La présente série d'articles a été produite pour résumer les connaissances actuelles au sujet d'interactions spécifiques entre des variables biotiques et abiotiques qui peuvent contribuer à déterminer la survie du saumon atlantique. L'évaluation des défis rencontrés sur les sites de fraie (siltation, oxygénation), dans les habitats nourriciers (substrat, interactions trophiques), dans les habitats d'hivernage (condition du courant, opportunités d'alimentation hivernale) et dans les environnements côtiers et océaniques (température de l'eau, prédateurs, parasites) suggèrent que tous les habitats requis par le saumon atlantique et tous les processus qui s'effectuent dans chaque habitat représentent des maillons critiques qui permettent à cette espèce de persister. Les pratiques de gestion employées durant la sélection artificielle des poissons, l'incubation, et l'introduction affectent aussi le succès des programmes de restauration. Parce que les facteurs limitants peuvent changer dans le temps et parce que notre capacité à intervenir dans certains habitats est limitée, la seule stratégie à notre portée est de continuer à accumuler des informations au sujet des processus qui déterminent la fragilité du saumon atlantique et, à la lumière de ces observations, enclencher des actions scientifiquement défendables où et quand c'est possible.

Introduction

Everything about Atlantic salmon (*Salmo salar*) once inspired a sense of grandeur; the potential size of individuals, the number of fish that roamed the rivers and the seas, and the wide distribution of the species. These fish also evoked images of majestic and pristine rivers, quasi-mythic journeys to the ocean and back to their original birthplace, and an instinctive determination to persist in spite of numerous challenges. These attributes fully justified the cultural, social, and economic status held by this species. The decline of Atlantic salmon across its range during the past three decades, despite the international ban on commercial harvesting on ocean feeding grounds and the implementation of numerous conservation programmes in rivers, now compels us to acknowledge the fragility of this species. The follow-

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D. Boisclair. Université de Montréal, Département de sciences biologiques, C.P. 6128, Succursale «Centre-ville», Montréal, QC H3C 3J7, Canada (e-mail: daniel.boisclair@umontreal.ca).

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ing series of papers represent a glimpse of the current knowledge on the effect of interactions between biotic or abiotic variables on Atlantic salmon.

Egg survival and embryo development

The survival and development of Atlantic salmon is affected by numerous physical conditions even before hatching. Experiments performed by Lapointe et al. (2004) to assess the relationship among egg-to-emergence survival, substrate composition, and hydraulic conditions suggest that a few percent of silt in reeds may have a strong negative effect on egg-to-emergence survival. This study further indicates that the magnitude of the effect of silt may increase with the sand content of the substrate. One consequence of this finding is that the interstitial flow required to maintain egg-to-emergence survival may vary with the relative contribution of silt and sand to the substrate. In addition to substrate composition and flow conditions, the supply of oxygen necessary for egg survival and embryo development may also depend on hydrological features. Youngson et al. (2004) estimated the impact of oxygen-poor, long-residence ground water on the survival and development of Atlantic salmon embryos. Their field experiments indicate that low levels of hyporheic oxygen may have a negative effect on embryos' survival and size, particularly when incubation occurs deep in the substrate. This study therefore underlines the potential importance of assessing the effect of long-term hyporheic ground water on the production of Atlantic salmon in rivers. In addition, it was noted that eggs laid near the surface of the substrate may suffer from physical disturbances. This also provides a new insight on the dilemma faced by spawners regarding the depth in the substrate at which eggs should be laid to maximize egg-to-emergence survival.

Interactions between phenotypes and environmental conditions for fry and parr

Some approaches that are employed to avoid problems caused by the harsh conditions that may occur during the incubation period include the use of in situ incubators designed to minimize egg disturbance and the stocking of fry or parr in rivers. Laboratory and field experiments showed that the rearing conditions (hatchery or stream) and the timing of fry introduction to a river relative to (*i*) the emergence of other groups of fry, (*ii*) water temperature fluctuations, or (*iii*) flow regime have a marked influence on fish size and survival (Letcher et al. 2004). These interactions do not only influence the fry stage but persist through time and could be perceived in the size, survival, and expression of life-history traits in parrs. Such information may influence the current stocking practices and may improve the success of fry introduction as a means to support conservation and restoration efforts. Although the manner and timing of fry introduction may be important, matching fish phenotypic attributes with environmental conditions may also contribute to the success of stocking operations. There are relatively few examples of tests of the relative ecological or physiological performance of fish with different phenotypes. Enders et al. (2004) compared the swimming metabolism of three phenotypes of Atlantic salmon parrs (wild, farmed, and domesticated) from Canada and Norway. In contrast with traditional respirometry studies that use quasi-laminar flows in tube respirometers, the experimental flows tested were turbulent. This study shows that the physiological costs of swimming against a turbulent flow is 2.4- to 4.0-fold higher than predicted by models developed using quasi-laminar flows. While the swimming metabolism did not vary between wild and farmed parr, both were significantly lower than swimming metabolism of domesticated parr, indicating that artificial selection may have a negative effect on the ability of domesticated parr to cope with turbulent flows. Whether or not all wild populations conform to a single respiration model is presently difficult to establish, because relatively little is known about the magnitude of the phenotypic differences that may exist among a larger number of natural populations of Atlantic salmon. In this context, Obedzinski and Letcher (2004) performed a series of common environment experiments intended to assess among-population phenotypic differences attributable to genetic variations. They found that conclusions about the existence or magnitude of phenotypic differences among five populations of Atlantic salmon might vary with the life stage considered (i.e., egg, alevin, early parr, late parr). Their work clearly shows that the study of phenotypic variations and stock differentiation not only requires the examination of numerous traits but that traits should also be examined at numerous life stages. Yet the source of this variation remains unknown. Determination of the relative effect of adaptations to river-specific environments and hatchery selection on genetically based phenotypic differences requires the study of the environmental conditions experienced by fish in rivers.

Parr distribution patterns and their consequences

The relationship between fish and environmental conditions may be described using habitat preference indices. For instance, environmental conditions used by Atlantic salmon aged 0–5 years in a subarctic river were determined by estimating their preference for specific ranges of water depth, flow velocity, and substrate composition during the summer, autumn, midwinter, and late winter (Mäki-Petäys et al. 2004). This field study shows that habitat preferences may vary among seasons, particularly for older parr that tend to move from rapid to low-flow velocities during the winter and spring. This change in the distribution of older parr may also modify the interactions between fish of different age classes. This study indicates that the proper analysis of fish–habitat interactions in rivers calls for age- or size-specific descriptions of the seasonal variations of the physical conditions required by Atlantic salmon. Although it is important from a management perspective to identify the environmental conditions preferred by fish, it is also useful to assess the consequences of environmental conditions on correlates of fish fitness.

Environmental conditions and habitat selection are expected to have a direct impact on fish foraging, growth, and survival. Girard et al. (2004) examined this issue and found that in the summer, habitats preferred by 0+ fish provided superior access to food (higher drift of invertebrates) and higher

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foraging rates than habitats avoided by these fish. Their study also showed than fish size, growth, and survival do not vary among habitats assigned different preference indices. While higher fish densities in preferred habitats are consistent with the predictions of an ideal free distribution, comparisons with other studies suggest that Atlantic salmon may shift from an ideal free to an ideal despotic distribution, depending on fish densities and habitat types. Hence, the study of the energetic consequences of fish distribution in rivers may require that ideal free and ideal despotic schemes be taken as complementary instead of mutually exclusive hypotheses.

Interactions between environmental conditions and habitat selection in the winter are generally anticipated to affect parr survival. However, experiments to quantify the effect of flow velocity and shelter availability on parr revealed that variations of environmental conditions in winter may not only affect parr survival but also their ability to maintain a given size or, in some cases, to maintain and even increase their energy density (Parrish et al. 2004). Similarly, Finstad et al. (2004) found that as the winter progresses, 2+ and 3+ parrs with low energy densities may be selectively removed from natural systems because of an energy-dependent mortality. This study also indicates that parr overwintering mortality is defined by a critical energy density and not by fish size. These observations suggest that management operations aimed at increasing the availability of conditions that would allow parrs to feed during the winter may also allow them to maintain or increase their energy density and to improve their survival during this period.

Life in coastal and oceanic habitats

The conditions encountered by smolts as they exit their native rivers differ from their original environment in terms of water temperature, water salinity, prey, predators, and parasites. The differences between riverine and coastal habitats represent a series of environmental stressors to which smolts must rapidly adapt. However, as emphasized by the review in Jonsson and Jonsson (2004), both coastal and oceanic habitats changed over the past few decades. More specifically, features such as the size of a proper thermal habitat for growth in the ocean may have significantly decreased during this period. This reduction, which may be a consequence of global climate change, may affect growth and survival and key life-history traits such as fish size and age at maturity. Niemelä et al. (2004) supported this view by showing that during the period of 1972–2003, part of the variation in salmon catches for stocks that showed no consistent trend of decline could be related to mean sea temperature in July during the year of smoltification. Global climate change was also invoked by Juanes et al. (2004) to explain a shift in the timing of the upstream migration of adults from numerous North American stocks during the past 23 years. Although the exact mechanism by which this shift occurs is not completely understood (changes in river discharge, river temperature, oceanic temperature), the timing of upstream migrations may affect the environmental conditions experienced by fish in rivers and the survival of mature fish.

Spawners

From a population dynamics standpoint, the most important contribution of spawners is the production of fertilized eggs. In many systems, a significant fraction of the adult population of Atlantic salmon dies after spawning. Nislow et al. (2004) developed a framework designed to identify the life-history interactions that may determine whether Atlantic salmon migrations result in the net importation or the net exportation of nutrients for freshwater systems. This study suggests that the low numbers of adults currently returning to spawn may not have a negative effect only on the number of eggs deposited in rivers, but also on the general productivity of the nursery areas, and consequently, on the growth and survival of fry and parr.

Conclusion

The present series of papers provides new knowledge about the impacts of interactions between biotic and abiotic variables on Atlantic salmon throughout their life cycle. These papers illustrate that all habitats required by Atlantic salmon and all processes that occur in each habitat represent a link in a chain of events that allows this species to persist. The relative importance of elements that contribute to the fragility of Atlantic salmon is difficult to define because of (*i*) the diversity of habitats required by these fish to complete their life cycle, (*ii*) the complexity of the interactions between biotic or abiotic variables in these habitats, and (*iii*) the range of spatial and temporal scales at which these interactions operate. The identification of key determinants at this point in the history of the species may be conjectural and futile. Limiting factors may change in time, and our ability to intervene in specific habitats is sometimes minimal. Unfortunately for scientists, managers, and Atlantic salmon, the only strategy within our reach may be to continue gathering information about processes that determine the fragility of Atlantic salmon populations and, in the light of these findings, implement scientifically sound actions wherever and whenever possible.

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Interactive effects of substrate sand and silt contents, redd-scale hydraulic gradients, and interstitial velocities on egg-to-emergence survival of Atlantic salmon (*Salmo salar*)[1]

Michel F. Lapointe, Normand E. Bergeron, F. Bérubé, M.-A. Pouliot, and P. Johnston

Abstract: We conducted laboratory incubation experiments with Atlantic salmon (*Salmo salar*) eggs to test a number of hypotheses concerning the relative sensitivity of the incubating eggs to variations in silt (diameter < 0.063 mm) in interaction with sand (0.63 mm < diameter < 2 mm) fractions in the incubating gravels, as well as to different strengths of local hydraulic gradients pushing flow across the egg pocket. Our results show that variations of only a few percent of silt content can strongly degrade survival to emergence. Higher silt loadings (>0.5%) are detrimental to survival for all substrate mixtures, except those that are very sparse in sands (<5%). For sand contents over 10%, an increment of 1% silt has over three times the effect on survival as a 1% increment in sand. Increasing hydraulic gradients had a positive effect on median survival, but the effect depended both on the details of the fines composition and on the gradient level. Our results suggest that silt loadings over 1.5% in redds cannot easily be mitigated by stronger gradients. Our data conclusively show that there is no single threshold interstitial flow velocity that insures survival to emergence. Even when maintaining a constant interstitial velocity, survival tended to reduce in higher fines-content substrate.

Résumé : Nous avons effectué en laboratoire une étude d'incubation d'œufs de saumon atlantique (*Salmo salar*) afin de tester la sensibilité relative des œufs aux variations du pourcentage de limon (le diamètre < 0,063 mm) et de sable (0,63 mm < le diamètre < 2 mm) dans le substrat d'incubation, ainsi qu'aux variations du gradient hydraulique. Nos résultats indiquent que des variations très faibles du contenu en limon réduisent fortement la survie à l'émergence. Des contenus en limon élevés (>0,5 %) réduisent la survie pour tout les substrats étudiés, sauf ceux ayant de très faibles contenus en sable (<5 %). Lorsque le contenu en sable est supérieur à 10 %, une augmentation de 1 % des limons a un effet sur la survie plus de trois fois supérieur à une augmentation comparable de sable. L'augmentation du gradient hydraulique augmente la survie médiane mais l'ampleur de l'effet dépend de la composition exacte en sédiments fins et du gradient hydraulique. Nos résultats suggèrent que des teneurs en limons supérieurs à 1,5 % sont difficilement compensables par un gradient hydraulique élevé. Les données montrent aussi l'inexistence d'un seuil unique de vitesse d'écoulement interstitiel permettant d'assurer la survie des œufs; même à vitesse intersticielle constante, la survie des œufs tend à diminuer avec une augmentation du contenu en fines.

Introduction

Assessing the quality of spawning habitat is of great importance for the management of salmonid populations in rivers. Current research suggests that spawning habitat quality cannot easily be summarized by a single metric; it is affected by multiple environmental controls operating at different physical and temporal scales. Redd site selection must not only ensure sufficient interstitial water flow locally around the egg pocket over the whole incubation period, its location within the river pattern must also minimize the vulnerability of egg pockets during seasonal extremes to freezing, scouring, and sediment entombment (Sowden and Power 1985; Prowse 2001; Lapointe et al. 2000). Nonetheless, for the purposes of habitat management, fines content within gravel–cobble substrate remains a primary predictor of

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M.F. Lapointe.[2] Department of Geography, McGill University, 805 Sherbrooke West, Montréal, QC H3A 2K6, Canada.
N.E. Bergeron, F. Bérubé, M-A. Pouliot, and P. Johnston. Institut national de la recherche scientifique (INRS), Centre Eau, Terre et Environnement, 880 chemin Sainte-Foy, bureau 840, C.P. 7500, Québec, QC G1V 4C7, Canada.

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[2]Corresponding author (e-mail: lapointe@geog.mcgill.ca).

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spawning habitat quality. This study aims to quantify the effects on reproductive success of interactions between sand and silt contents combined with the effects of variations in strength of local hydraulic gradients pushing flow across the egg pocket (here silts refer to particle sizes under 0.063 mm).

The detrimental effects of excessive fine sediment on substrate permeability, intergranular flow velocities, and resultant survival of salmonid embryos and (or) sac fry have been documented in numerous laboratory studies (Peterson and Metcalfe 1981; Tappel and Bjornn 1983; Young et al. 1991). Unfortunately these studies refer to a range of very broad measures of fines content, such as total fraction under 2 or 8 mm, and most fail to explicitly account for the large differences in inherent permeability among finer alluvial fractions. Yet, the detrimental effects for reproductive success of a unit mass of alluvial silt (diameter (D) under 0.063 mm) may be much greater than that of an equivalent mass of sand. Because the permeability (or hydraulic conductivity) of uniform granular material varies with the square of particle diameter (Vukovic and Soro 1992), relative permeability varies, for example, 30-fold between pure 1-mm coarse sand and 0.15-mm fine sand and 30-fold again between fine sand and 0.03-mm silts. While Peterson and Metcalfe (1981) acknowledged, through their "sand index" (see Methods), the greater effect on reproductive success of fine sand (D between 0.06 and 0.5 mm) compared with coarse sands (D between 0.5 and 2 mm), no extant study has determined threshold values of silt content for egg survival. Although absolute silt content in gravel alluvium is usually very low, it is spatially variable and can locally reach a few percent in some salmon rivers draining friable, fine-textured parent rock (Wilson 2003).

From physical principles, sediment size composition and permeability affect intergranular flow rates (which control transport of oxygen and removal of metabolic wastes). A number of studies have thus cited, as thresholds for reproductive success, minimum intergranular flow velocities rather than maximal fines contents (Wickett 1954; Cooper 1965). Based on Darcy's law

$$(1) \qquad V = -K(\Delta H/\Delta X)$$

the bulk flow velocity (V, also called specific discharge) through the spawning gravel is a function, on the one hand, of the substrate hydraulic conductivity (K) controlled by grain size distribution and packing and, on the other hand, by the strength of the gradients ($\Delta H/\Delta X$) in hydraulic heads (H) driving interstitial flow through the riffle substrate over a distance ΔX. In theory, a sufficiently strong hydraulic gradient can thus compensate for a low permeability substrate and yield any level of interstitial velocity required to transport oxygen and wastes. Moreover, shallow sub-bed hydraulic gradients vary spatially over rivers, partly controlled by channel and bedform morphology (Cooper 1965; Geist and Dauble 1998; Geist 2000). There is indirect evidence that spawners may select for local gradient conditions in addition to substrate composition. Bigger, more complex spawning bars, often associated with stronger hyporheic gradients, in some cases with suboptimal substrate, appear to be preferred spawning sites for certain salmonids (Geist and Dauble 1998; Baxter and Hauer 2000; Coulombe-Pontbriand and Lapointe 2004).

However, even if strong gradients produce adequate interstitial flow rates, embryo emergence from the substrate may be hindered if substrate fines content is too high, leading to smaller pore spaces and stronger compaction. Thus, it is unclear whether reproductive success depends solely on interstitial flow velocity, irrespective of substrate fines content and the extent to which fish selection of spawning beds under stronger interstitial gradients can compensate for high substrate fines content. To test these questions, we conducted laboratory incubation experiments to clarify the relative sensitivity of reproductive success (defined here as egg to emergence survival) to varying proportions of sands and silts under different hydraulic gradients and resultant flow velocities across the egg pocket.

Three hypothesis were tested: (*i*) over a range of sand contents, variations in silt contents have a clear effect on reproductive success, and reproductive success is significantly more sensitive to silts than to similar amounts of sands; (*ii*) for any given substrate mixture, survival increases with the strength of the local hydraulic gradient driving flow across the egg pocket; and (*iii*) while interstitial flow velocity integrates the effects of substrate size and local hydraulic gradients, it cannot on its own completely predict reproductive success; at any given interstitial velocity, survival to emergence still varies with the amount of fines present in the incubating substrate.

Methods

A series of laboratory experiments were conducted between November 2002 and March 2003 in the Laboratoire régional des sciences aquatiques (LARSA) at Laval University, Québec (Canada). In these experiments, Atlantic salmon (*Salmo salar*) eggs were incubated in cylinders containing varying sediment size mixtures and subjected to different hydraulic gradients. Sixteen sediment mixtures were created using an orthogonal design, made up of four percentages of sand and four percentages of silt, each of which were subjected to three different hydraulic gradients ($\Delta H/\Delta X$= 0.009, 0.006, 0.012). (Here, a gradient of 0.012 or 1.2% represents a drop of 1.2 cm of hydraulic head over a 1-m downflow path).

Experimental sediment mixtures consisted of a common control mixture of gravels to which was added varying combinations of sands and silts. The coarse control gravel did not include sediment smaller than 2 mm and its grain size distribution (10% under 4 mm, 25% under 10 mm, 50% under 26 mm, and 90% under 55 mm) was selected to be broadly representative of a typical Atlantic salmon redd in Quebec streams. The proportion of sand in a mixture was quantified with the sand index (SI) developed by Peterson and Metcalfe (1981)

$$(2) \qquad SI = (S_c/16 + S_f/8)$$

where S_c and S_f are, respectively, the percentages of coarse sand (0.5–2 mm) and fine to medium sand (0.06–0.5 mm). Owing to space and time limitations, we could not test independently varying combinations of these two sand fractions; in all mixtures, the ratio of coarse sand to fine sand was held constant at 3.3, again a typical value for riffle alluvium in Quebec salmon rivers.

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The SI values tested in this experiment (0.5, 1.0, 1.5, 2.0) were selected to be representative of the range of values encountered in natural salmon streams. According to Peterson and Metcalfe (1981), embryo survival is generally excellent when SI is <1.0, whereas it is very poor when SI is >1.5. These authors, however, gave no details on the range of applicability of this threshold in terms of silt levels or gradient conditions. For each SI value, four different percentages of silt representative of the range of values (0.2%, 1.2%, 2.2%, 3.2%) generally found in Quebec salmon streams were tested. To assemble each mixture, we weighed and thoroughly mixed its three components (control gravel, sands, and silts) while dry, in the order of finer fractions to coarser fractions. Resultant mixtures were then carefully inserted in layers in a polymer cylinder (diameter 15 cm × height 50 cm).

The porosity (p) of each mixture was determined in the laboratory from

$$(3) \qquad p = V_e/V_t$$

where V_e is the volume of water needed to saturate the total volume (V_t) of the cylinder containing the dry sediment mixture. Three replicate groups of 16 cylinders, each group covering the range of study mixtures, were then installed in separate basins to undergo different gradient conditions. Each basin was divided into an outer and a central section. The cylinders were installed in the outer section, each cylinder being connected to the central section by a 2-cm diameter pipe located immediately above the bottom of the cylinder (Fig. 1). A hydraulic gradient was created inside the cylinders by maintaining different water levels in the outer and central sections of the basin. All flow paths between these two sections, other than from the top of each cylinder to its outlet pipe, were carefully sealed. All cylinders inside each of the three basins were thus subjected to exactly the same hydraulic gradient.

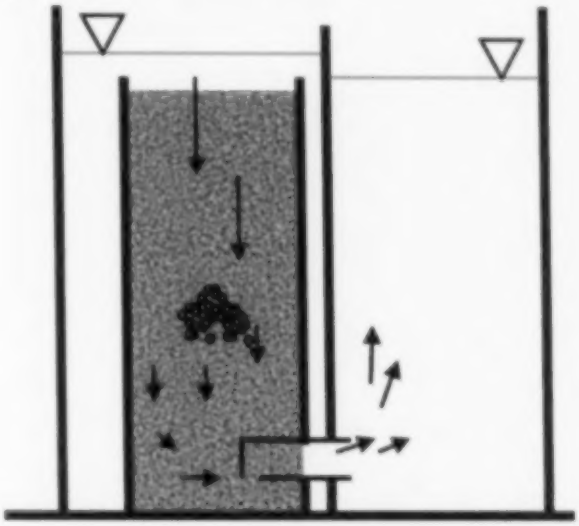
The mean velocity in pore spaces, also called mean intersticial velocity, (V') for each sediment mixture and gradient was measured from

$$(4) \qquad V' = V/p = Q/(Ap)$$

where Q is the water discharge coming out of a cylinder, V is the bulk velocity or specific discharge used in Darcy's law (eq. 1), p is the porosity of the sediment mixture, and A is the surface area of the cylinder. Water discharge in a cylinder was determined by attaching a plastic bag to the end of the pipe located in the central section of the basin and averaging replicate measurements of the total volume of water flowing into the bag over a given period of time. The median hydraulic gradient used in these experiments (0.006) produced a flow velocity in the interstices of 0.015 cm·s^{-1} in a cylinder containing only the clean control mixture. This value is typical of flow velocities measured in salmonid redds from which fine sediments were winnowed by the digging action of the female fish.

The Atlantic salmon eggs used in the experiment were provided by the Société Cascapédia and came from adults of the Cascapédia River (Québec, Canada). Within 24 h of fertilization, all eggs were water-hardened, transported to the laboratory in water-filled mason jars maintained at a temperature of 4 °C, acclimated to water basin temperature (8.8 °C) by increasing water temperature at a rate of 1 °C·h^{-1}, and placed in the experimental incubating substrates. A control batch of fertilized eggs was kept aside in an incubator to determine the percentage of nonviable eggs. The percentage of nonviable eggs was under 10% and no correction was applied to survival to emergence data. For each cylinder, a 15-cm-thick layer of sediment was first put at the bottom of the cylinder. Then, 100 eggs were distributed over the gravel surface and covered by another 15-cm-thick layer of sediment. This manipulation was done while the cylinders were filled with water to reduce damage to the eggs.

Fig. 1. Diagram showing one of the cylinders used to incubate Atlantic salmon (*Salmo salar*) eggs. Side view (elevation). Large, open triangles denote water levels in the different sections of the basin.



Unchlorinated water flowing through the cylinders was maintained at a temperature of 8.8 °C throughout the incubation period, which started on 7 November 2002. Starting 10 days prior to the expected date of the beginning of emergence at the end of January, each cylinder was inspected daily for emerged fry. On each occasion, emerged fry were counted and removed. Survival to emergence was measured as the total number of fry collected from each cylinder over the incubation period.

Results

Interactive effects of silt and sand contents on survival

Curves of mean survival rates averaged over the three study gradients are presented as a function of % Silt and % Sand (or equivalent SI values; Fig. 2). Isolines representing percent survival were interpolated using a distance-weighted least squares procedure. The overall trends of the contours reveal an interaction between the effects of silt and sand contents on survival. While scarcity of data points limits our ability to resolve thresholds with great precision, large silt contents have negligible effect on mean survival at SI values under approximately 0.75 (percent sand under 10%). In contrast, the effects of rising silt content is quite marked at sand

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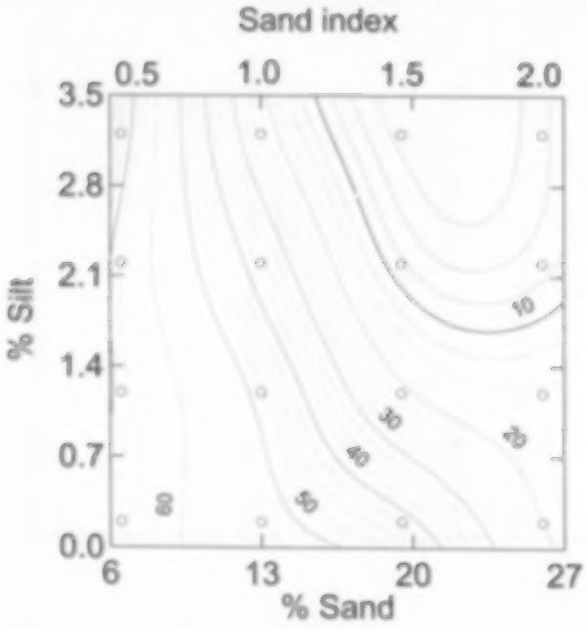
Fig. 2. Percent survival (numbers on lines) to emergence of fry averaged over the three study gradients as a function of % Sand (or Sand Index, top) and % Silt. Circles locate data points.



indices greater than 1.25 (percent sand over 16%). Similarly, with increasing silt contents, a given value of SI is associated with progressively lower survival rates.

A simple regression model based solely on substrate texture (eq. 5) and neglecting gradient values, with highly significant ($p < 0.0003$) SI and sand–silt interaction terms, predicted 50% (adj R^2) of the variations in experimental survival data. The sand–silt interaction term adds 6% to the variance explained by SI as single predictor.

$$(5)\quad \%\,\text{Survival} = 83 - 29(\text{SI}) - 6(\text{SI} \times \%\,\text{Silt}),\qquad R^2 = 50\%,\ p = 0.00001$$

or equivalently

$$\%\,\text{Survival} = 83 - 2.3(\%\,\text{Sand}) - 6(\%\,\text{Sand} \times \%\,\text{Silt})$$

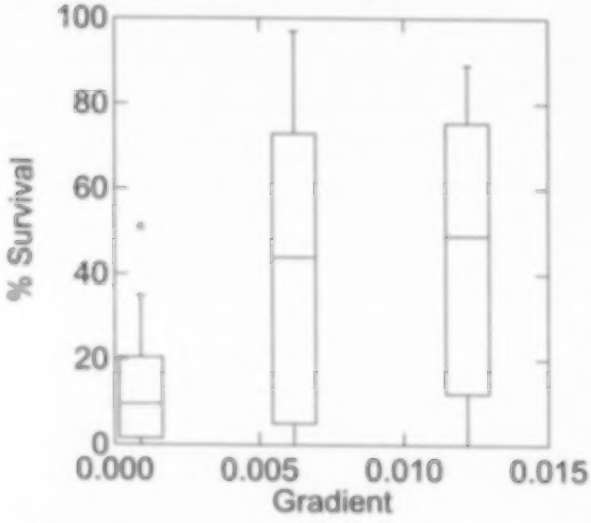
Over much of the mixture space corresponding to moderate to high sand contents (i.e., for SI between 0.8 and 1.6 or percent sand in the range of 10%–22%), the isolines of % Survival remain more broadly parallel (Fig. 2) For this range, a simplified linear model (eq. 6) in sand and silt (without interaction term) captures 52% of the variation in mean survival across the study gradients

$$(6)\quad \%\,\text{Survival} = 103 - 10(\%\,\text{Silt}) - 3(\%\,\text{Sand}),\qquad p < 0.00001$$

Effects of changing hydraulic gradient on egg-to-emergence survival

Increasing hydraulic gradients had a positive but somewhat nonlinear effect on median survival over all sediment mixtures tested (Fig. 3). The increase in survival associated with a given increment in gradient depends both on the details of the fines composition as well as on the level of gradient (as illustrated in Figs. 4*a*, 4*b*). The interpolated contours (Fig. 4*a*) reveal that increasing gradients (from low to mid-range, yielding a 40% median increase in survival overall; cf. Fig. 3) broadly increase survival rates across the spectrum of composition, except at the very highest sand content tested. The most pronounced effect of ramping hydraulic gradients from low to mid-range first occurs in clean (low sand, low silt) mixtures, where the increment in survival exceeds 50%.

Fig. 3. Box plots of survival to emergence of fry as a function of imposed hydraulic gradient. The middle line represents the median survival, the box splits the remaining halves again, the whiskers are 1.5 times the interquartile range, and the asterisk is less than three times the interquartile range.



Increasing hydraulic gradient by a further, comparable increment (from the mid-range (0.005) to the highest value tested (0.012)) only enhanced median overall survival by a few percentage points (cf. Fig. 3). However, this had a strong beneficial effect (Fig. 4*b*) for the subset of mixtures with high sand but lower silt contents, where survival increased by 20%–50%. We summarize the contrast in overall survival response to increasing gradients between silt-rich (Fig. 5*a*) and silt-poor mixtures (Fig. 5*b*), with arbitrary separation at 1.5% silt. While median survival increases continuously with gradient across all silt-poor mixtures, the median survival response of silt-rich samples is muted as gradients are increased between low and mid-range and are nonexistent between mid-range and high gradients.

Adding hydraulic gradient terms to the sediment composition predictors in eq. 5 increases by 27 percentage points the variance explained in the survival data (i.e., from 50% (eq. 5) to 77% (eq. 7)). This regression model incorporates only three highly significant ($p < 0.00001$) predictors: gradient, % Sand, and an interaction term between gradient and fines content (% Sand × % Silt).

$$(7)\quad \%\,\text{Survival} = 51 - 2(\%\,\text{Sand}) + 5070\,(\text{Gradient}) - 69(\text{Gradient} \times \%\,\text{Silt} \times \%\,\text{Sand}),\qquad R^2 = 77\%,\ p < 0.00001$$

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Fig. 4. Percent change of survival (numbers on lines) to emergence resulting from an increase of gradient (*a*) from low- to mid-level gradients and (*b*) from mid- to high-level gradients.

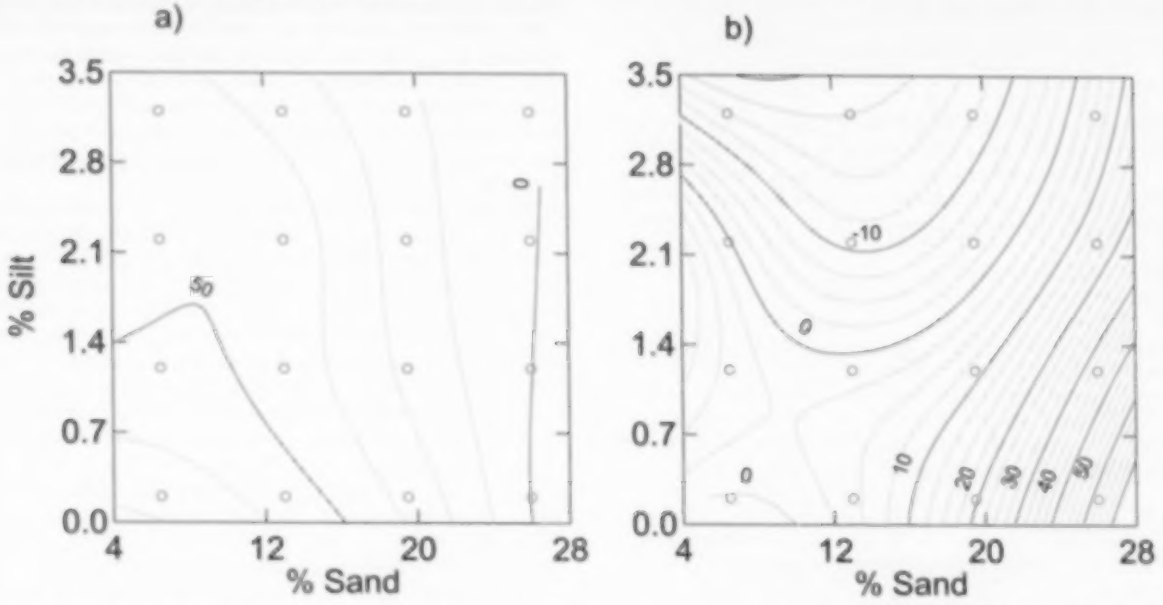
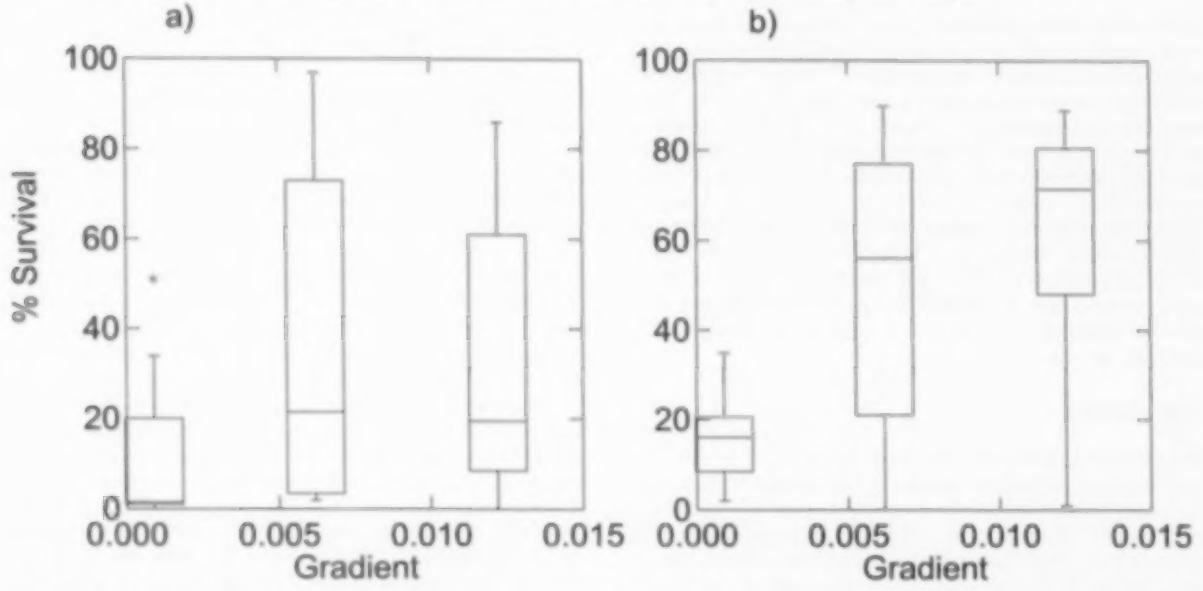


Fig. 5. Box plots showing effects of increasing the imposed hydraulic gradient on survival to emergence for (*a*) silt-rich (>1.5%) and (*b*) silt-poor (<1.5%) sediment mixtures. The middle line represents the median survival, the box splits the remaining halves again, the whiskers are 1.5 times the interquartile range, and the asterisk is less than three times the interquartile range.



Interstitial velocities and survival

As discussed in the context of Darcy's law (eq. 1), it may be expected that the combined effects of fines content and hydraulic gradient on survival can be integrated through the intensity of interstitial velocities, V' (eq. 4), flowing through the egg pocket. The associations among interstitial velocity, percent sand, and observed survival in our two experiments are illustrated (Fig. 6). Although survival increases with velocity for any sediment composition, at any given value of interstitial velocity lower survival rates occur with progressively higher sand contents (Fig. 6; note that isolines in the top right part of the panel are extrapolated beyond our data). Equation 8 predicts 70% of the variation in experimental survival rates based on velocity and fines content terms (% Sand and sand–silt interaction terms, three predictors that are each highly significant individually).

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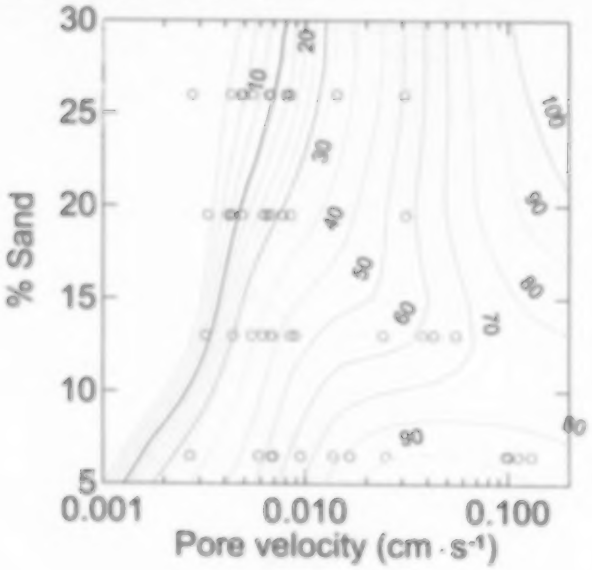
Fig. 6. Isolines of percent survival (numbers on lines) to emergence of fry as a function of interstitial pore velocity and sand content. Circles denote data points.



$$(8)\quad \%\,\text{Survival} = 141 + 36\log(V^{*}) - 1.5(\%\,\text{Sand}) - 4.1(\%\,\text{Sand} \times \%\,\text{Silt}),\quad R^2 = 70\%,\ p < 0.0001$$

While there is no correlation among sand, silt, and gradient in our experimental design, there is a modest negative correlation (–0.45) between the variables % Sand and observed interstitial velocity in the data (as also seen in Fig. 6). However, this correlation was too weak to cause multicollinearity problems in estimating equation 8; all tolerances were greater than 0.65 and all coefficient estimates had individual p values under 0.02. While velocities range over two orders of magnitude, observed substrate porosities (at 28% ± 3%) vary weakly across our mixtures. Thus, bulk velocities V were strongly correlated to interstitial velocities V^{*} ($V \equiv 0.28V^{*}$) in our data set so that we cannot clarify if any of the two measures of intergranular velocity is superior to the other as a predictor of survival.

Discussion

The relative effects of silt versus sands

Although a substantial portion of the silt and sand content is usually flushed out of fresh redd substrate by female digging activity (Kondolf et al. 1993; Montgomery et al. 1996), appreciable reinfiltration of fines around egg pockets can occur in fines-rich stream systems over the many months of the incubation period (Everest et al. 1987). Our results indicate that for the particular gravel mixture tested, high silt loadings are detrimental to survival for all substrate mixtures except those that are very low in sand content (<5%). For sand contents over 10%, an increment of 1% silt has over three times the effect on survival as a 1% increment in sand (eq. 6). Our data indicate that except for mixtures with low sand contents, variations of only a few percent of silt content in spawning substrate over the course of incubation can strongly degrade survival from egg to emergence. For example, at 15% sand (SI of 1.25) mean survival decreases from 60% to 20% as silt content increases over the range 0%–4%. Recall that only one control gravel mixture (fractions courser than 2 mm) was tested; this was selected to be typical of salmon spawning substrate. Reported threshold values might vary somewhat for other gravel compositions, especially if the percentages of granules (2–4 mm) were very different than that tested (10%).

The interaction between sand and silt content evidenced in Fig. 2 and eq. 5 appears to reflect differences in resultant pore space organization under the effect of seepage forces caused by interstitial flow. At very low sand contents, even large masses of silt particles may be free to rearrange themselves slightly within the gravel framework, opening preferred routes for intergranular flow and maintaining substantial flow and emergence routes across the egg pocket. (In none of our experiments, however, did silt leach out of the cylinders into the receiving basin.) However, at higher sand contents, ubiquitous sand particles obstruct much of the intergravel space, allowing the silts to better bridge the remaining pore spaces. This interaction inhibits the establishment of connected macropores under greater seepage forces, reducing flow rates as well as hindering emergence more effectively.

Our data and regression model (eq. 5) also allows us to refine the interpretation of Peterson and Metcalfe's (1981) SI (eq. 2). For example, with less than 0.5% silt, an SI of 1.0 (Peterson and Metcalfe's nominal threshold separating good from mediocre substrate) yields an average survival of 70% over the range of four gradients tested. However, at 3% silt, survival is only 40% at SI = 1.0.

The interactive effects of hydraulic gradient and fines content on survival

Our results confirm that variations in local hydraulic gradients across redds, typically associated with variations in channel morphology (Cooper 1965; Baxter and Hauer 2000), could potentially be exploited by salmon to enhance reproductive success. However, they also highlight the complex, multifactorial nature of spawning habitat quality indices. While Peterson and Metcalfe (1981) state that SI values greater than 1.5 correspond to poor spawning substrate, at the highest gradient we tested (0.01), survival reached 60% in a mixture with SI of 2.0 and with low silt loading (<0.5%).

The data show that there is no single, threshold interstitial flow velocity that insures survival from egg to emergent fry; fines content also matters. For example, a 0.01 cm·s^{-1} interstitial velocity through a 6% sand mixture is associated with a 60% mean survival over the range of study gradients. However, when sand content is as high 26%, the same interstitial velocity is associated with only 20% mean survival. This is consistent with the view that fines, in addition to their effect on flow rate and hence potential metabolite transport rate, have mechanical effects on embryo development (such as membrane abrasion or hindrance to emergence).

Finally, the results indicate that the silt fraction plays a role in modulating how higher hydraulic gradients affect survival. As seen above, survival in high sand-loading mixtures can be enhanced at high gradients, as long as silt levels are relatively low. However, our results suggest that high silt, as-

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sociated with moderate to high sand loadings in redds, cannot as easily be mitigated by stronger gradients, at least within the range tested. One possible implication of this is that in rivers with very high suspended silt transport regimes, particular riffle zones with unusually high subsurface hydraulic gradient conditions may not be as important to stock reproduction as they may be in sand-rich, low-silt systems.

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Correction after posting

After this article was posted, it came to our attention that the y axis of Fig. 5 (which read % Silt) in the Results section was mislabelled. This figure has now been corrected.

The paper was originally posted at 0600 on 10 February 2005. The correction was posted at 1000 on 17 February 2005.

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Long-residence groundwater effects on incubating salmonid eggs: low hyporheic oxygen impairs embryo development[1]

A.F. Youngson, I.A. Malcolm, J.L. Thorley, P.J. Bacon, and C. Soulsby

Abstract: Atlantic salmon (*Salmo salar*) ova were incubated at a range of burial depths (50–300 mm) in a set of test arrays inserted at previously used redd sites in a near-pristine stream. Oxygen saturation and electrical conductivity of hyporheic water (obtained 0.5–1.0 m distant from each array from a depth of 200–300 mm below streambed level) were determined at ~2-week intervals over the incubation period (November–March). The test arrays were recovered from the streambed in mid-March, and thereafter, the eyed ova were incubated in surface water until hatch (24 March – 17 April). Embryo survival rates, hatch date, and alevin size differed among and within arrays. Mean alevin body size varied markedly among incubation groups (length, 14.9–20.8 mm; dry mass, 3.9–7.7 mg). Within arrays, embryo size varied with burial depth on fine spatial scales (approximately 50 mm); greater burial depth tended to be associated with smaller size. Among arrays, embryo size at the 250-mm depth was correlated with oxygen saturation of hyporheic water. Across all sites, oxygen saturation of hyporheic water decreased with greater conductivity, indicative of the presence of groundwater. Variation in embryo size was therefore linked with variation in the local dominance of deoxygenated groundwater in the hyporheic zone.

Résumé : Nous avons incubé des oeufs de saumons atlantiques (*Salmo salar*) à des profondeurs diverses (50–300 mm) dans des dispositifs expérimentaux dans des gravières utilisées précédemment dans un cours d'eau aux conditions peu modifiées. Nous avons mesuré la saturation en oxygène et la conductivité électrique de l'eau hyporrhéique (à 0,5–1,0 m de chaque dispositif expérimental à une profondeur de 200–300 mm sous le niveau du lit du cours d'eau) à des intervalles de ~2 semaines durant la période d'incubation (novembre–mars). Les dispositifs expérimentaux ont été retirés du gravier à la mi-mars et les oeufs, dont les yeux étaient apparents, ont été incubés dans de l'eau de surface jusqu'à l'éclosion (24 mars – 17 avril). Les taux de survie des embryons, les dates d'éclosion et les tailles des alevins varient à l'intérieur d'un même dispositif et d'un dispositif à un autre. La taille corporelle moyenne des alevins varie considérablement d'un groupe d'incubation à un autre (longueur, 14,9–20,8 mm; masse sèche, 3,9–7,7 mg). Dans les dispositifs, la taille des embryons varie en fonction de la profondeur d'incubation sur des échelles spatiales fines (environ 50 mm); les profondeurs plus grandes ont tendance à être associées aux tailles réduites. La taille à une profondeur de 250 mm dans les dispositifs est en corrélation avec la saturation en oxygène de l'eau hyporrhéique. Dans tous les sites, la saturation en oxygène de l'eau hyporrhéique est fonction inverse de la conductivité, ce qui indique la présence d'eau souterraine. La variation de la taille des embryons est donc liée à la variation de la prédominance de l'eau souterraine désoxygénée dans la zone hyporrhéique.

[Traduit par la Rédaction]

Introduction

Stream-spawning salmonids place their ova in nests excavated in the gravels of the substream hyporheic zone where surface water and groundwater mix. Ova are exposed to the hyporheic environment for a protracted period, which may extend for 5 or 6 months before hatch in the case of autumn spawners. Incubating ova are passively dependent on intragravel flow of hyporheic water for the delivery of dissolved oxygen necessary for survival (Hanor and Garside 1976; Rubin and Glimsater 1996; Malcolm et al. 2003*a*) and normal development (Alderdice et al. 1958; Silver et al. 1963; Garside 1966). Impaired development of incubating ova is often attributed to low rates of surface water percolation to redd gravels. In particular, reduction in percolation caused by the infiltration of fine sediment into the previously open

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A.F. Youngson[2] and J.L. Thorley. FRS Freshwater Laboratory, Faskally, Pitlochry, Perthshire PH16 5JL, UK.
I.A. Malcolm and C. Soulsby. Department of Geography and Environment, University of Aberdeen, Aberdeen AB9 2UF, UK.
P.J. Bacon. CEH Banchory, Banchory, Aberdeenshire AB31 4BW, UK.

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[2]Corresponding author (e-mail a.youngson@marlab.ac.uk).

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matrix of redds is often implicated (Chapman 1988; Reiser and White 1988; Rubin 1998). The findings of both Sowden and Power (1985) and Peterson and Quinn (1996), however, are contrary to this concept. They concluded that gravel composition was not the dominant control on the condition of the intragravel environment as it affected survival of ova at their sites and, therefore, some other factor was involved.

The groundwater component of hyporheic water is characterised by low dissolved oxygen as a result of chemical reduction during passage through soils (Freeze and Cherry 1979). In a previous study, we demonstrated from field experiments that the performance of brown trout (*Salmo trutta*) ova in a degraded agricultural stream was strongly associated with the hydrology and hydrochemistry of the hyporheic zone (Malcolm et al. 2003*b*, 2004). Groundwater dominance in the vicinity of the ova, or episodes of groundwater intrusion forced by changes in hydrological conditions, markedly affected both the survival of ova and the development of those that survived. Effects were shown to vary with burial depth at individual redd locations and to vary markedly at a reach scale among sites on fine (metre) spatial scales.

In a following study (Malcolm et al. 2004), we examined Atlantic salmon (*Salmo salar*) ova at a single spawning reach in a pristine gravel-bed stream, the Girnock Burn in northeastern Scotland, which is also the site of the present study. The reach selected had a history of intensive use by spawners extending over many years and had previously shown high levels of ova mortality in an exploratory excavation of a naturally spawned redd. A field experimental approach was used to demonstrate that the presence of groundwater had a marked effect on ova survival at some locations within the reach and, again, that the hydrology and hydrochemistry of the hyporheic zone varied markedly at fine spatial and temporal scales.

An understanding of ova survival and environmental controls on survival is important from a practical perspective in any location where the numbers of ova being spawned limits juvenile recruitment. Equally, any sublethal impairment of embryo development caused by exposure to low oxygen levels (Shumway et al. 1964; Rubin and Glimsater 1996; Malcolm et al. 2003*b*) is likely to be a determinant of individual post-emergence fitness and, therefore, recruitment. In addition, because of the site-specific nature of hydrological controls on the hyporheic environment, mortality or fitness effects probably vary among families, and this is expected to reduce effective population size (Ryman 1991).

In the present study, we examine ova survival and embryo development at a set of spawning locations distributed widely throughout the Girnock Burn. Vertical arrays of test groups of fertilised ova were inserted into simulated redds constructed using streambed gravels in known spawning locations used in previous years. Ova survival and the condition of embryos were assessed at hatch time and evaluated against hyporheic water quality measurements made over the incubation period.

Materials and methods

Study site

The site of the study was the Girnock Burn, a tributary of the River Dee in Aberdeenshire, Scotland, UK (Fig. 1). Patterns of spawning and habitat use by adult Atlantic salmon have been previously documented (Moir et al. 1998). The characteristics of the catchment have been described in detail elsewhere (Malcolm et al. 2002). Coarse gravels and coarse sands dominate spawning gravels, creating a bimodal sediment distribution with a median particle size of 21 mm. Fines content (<1 mm) was notably low at 5.4% (Moir et al. 1998).

Ten locations were chosen for study from a larger set of redd sites that had been documented photographically at spawning time in previous years. The locations were chosen to be representative of all sites and, while constrained by the patchy distribution of spawning habitat, were distributed relatively evenly along the stream's length (Fig. 1). The locations were assigned numerical codes allocated on the basis of a larger set of hyporheic sampling locations.

Fig. 1. Map showing the location of the Girnock Burn catchment (Aberdeenshire, Scotland, UK), topographical features, and sampling locations.

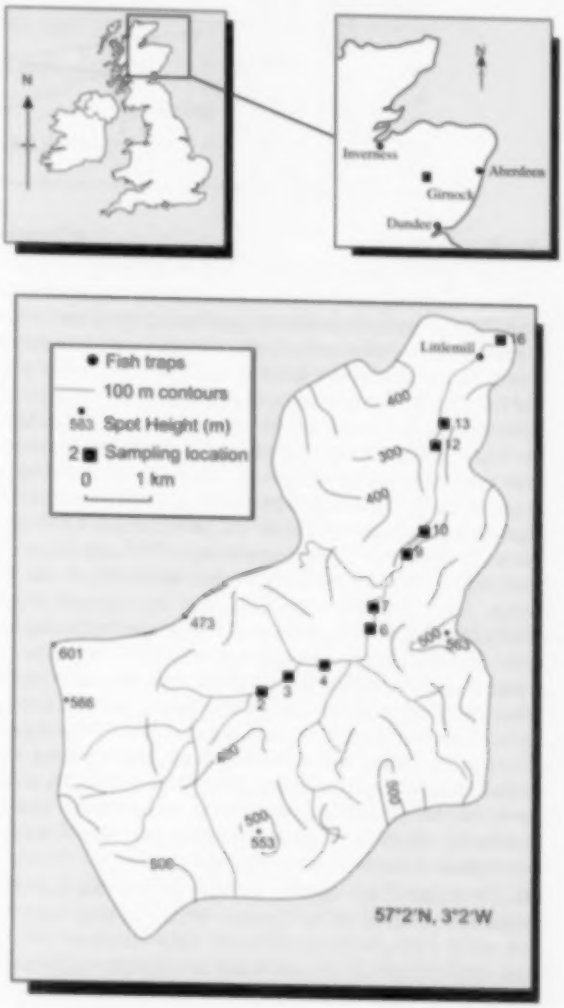

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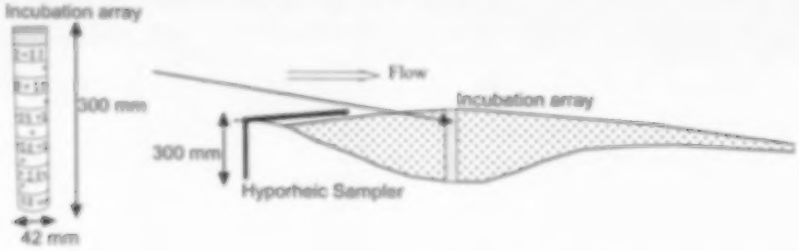
Fig. 2. Diagram showing an array of ova containers inserted in the streambed.



Methods

In June 2002, several months before spawning time, a hyporheic sampling tube constructed from 6 mm internal diameter (ID) polyethylene tubing, perforated over the lowest 100 mm and shielded with a fine mesh, was inserted to 300 mm below streambed level at each location using a removable, hollow steel driver and disposable drive point. In October 2002, 1 month before spawning time, simulated redds were prepared on previous redd sites. Using photographs as a reference, precision of placement was estimated as approximately 0.3 m. A draw hoe was used to prepare an elongated depression (0.5–1.0 m, maximum depth >300 mm) in the streambed. An insert comprising a 300-mm length of plastic pipe of 80 mm ID was located vertically in the depression, flush with the streambed, and the depression was backfilled to the natural profile of the streambed using the coarser fraction of the excavated gravel (>10 mm). The insert pipe was temporarily blanked off with plastic sheeting to keep the interior space free of extraneous gravel. The inserts were located within approximately 1.5 m of the hyporheic sampling tubes, but >0.5 m distant. This spacing was intended to minimise disturbance of hyporheic gravels in the vicinity of the samplers during redd construction and to minimise the effect of subsequent hyporheic water sampling on conditions within the artificial redds.

On 7 November, the eggs of a single female that had been captured and retained at the Girnock Burn fish trap were fertilised using a single male and were water-hardened for approximately 30 min in stream water at ambient temperature (3.5 °C). Over the remainder of the same day, the eggs were transported to the study sites in stream water (with intermittent refreshment), split among groups, combined into vertical arrays, and located into the prepared redd locations.

Stacking plastic containers that screwed together were used to hold egg groups. The internal height of each container was 22 mm and its volume was 30.5 mL. The base was 42 mm in diameter and accommodated >20 ova in a single layer. The external height of each unit was 30 mm, and when screwed together, 12 units combined to form a vertical array 300 mm in height (Fig. 2). The total size of the array was designed to span the range of natural burial depths characteristic (Crisp and Carling 1989) of the 2-sea-winter Atlantic salmon (body length approximately 700 mm) that dominate spawning in the Girnock Burn.

The uppermost container was blanked off with stream gravel. Twenty eggs (double-counted) were placed in the container below it and in each alternate container thereafter. Each vertical array therefore contained six groups of eggs lying at depths of 50, 100, 150, 200, 250, and 300 mm below streambed level. The intervening spacer units were void and served to isolate egg groups from one another and to prevent vertical exchange of intragravel water among units. Units containing eggs were perforated with a symmetrical array of 20 mm × 6 mm diameter holes; 20% of the internal wall space of each container was therefore void. Each container was lined with a collar of plastic 4-mm mesh (Netlon) to prevent ova from rolling into and occluding the holes in the container wall. Spacer units were drilled with paired holes, which served to vent trapped air when the array was immersed in the stream.

The completed arrays containing the fertilised ova were inserted into the prepared inserts on the redds, flush with the streambed. The insert was then withdrawn from around the array and any resulting gaps were infilled with coarse gravels (>4 mm) before the area was levelled off. After ova had been allocated to the arrays, the residual group of 347 ova was retained as a control in identical containers in a secure facility fed by surface stream water at Littlemill (Fig. 1).

All container arrays were recovered on 12 March (after 125 days of incubation), before hatching but after the "eyed" stage of development when ova become robust to handling. Dead eggs were counted and classified, where possible, according to the stage of development of the dead embryo. Surviving eggs were transferred to the holding facility containing the controls and were maintained in their original containers in surface water until hatching occurred. At hatch time, individual alevins were measured (length), weighed (combined body and yolk mass), and frozen in individual sealed containers. The bodies of 10 individuals sampled from each group were dissected from the yolk sac in a partially frozen state and freeze-dried. The small masses involved required that the bodies and yolk sacs of individuals were combined within groups to obtain group values (i.e., mean only) for the dry mass of both tissue components.

Ova/alevin groups have been coded according to location code and burial depth for presentation purposes. Thus, for example, an ova group located at location 6 to a depth of 150 mm is coded 6:150.

From November 2002 to March 2003, hyporheic water was sampled at each location at approximately 2-week intervals; 200 mL was withdrawn from sampling tubes under slight negative pressure. At each location, measurements were obtained for temperature (±0.1 °C), conductivity (±0.1 $\mu S \cdot cm^{-1}$), and dissolved oxygen (DO; ±0.1 $mg \cdot L^{-1}$) in both hyporheic and surface waters using a mercury thermometer, a Hanna HI 9033 conductivity meter (Hanna In-

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Table 1. Frequency of survival at excavation date for groups of 20 ova.

Incubation depth (mm)	Location code number									
	2	3	4	6	7	9	10	12	13	16
50	0	0	1.0	0.65	1.0	0	0	1.0	0	0
100	1.0	0.95	1.0	1.0	0	0.95	1.0	1.0	1.0	1.0
150	1.0	0.95	1.0	1.0	0	1.0	1.0	1.0	1.0	1.0
200	1.0	1.0	1.0	1.0	0	1.0	1.0	1.0	1.0	1.0
250	1.0	0.95	0.9	1.0	0	1.0	1.0	0.95	1.0	1.0
300	1.0	0.95	1.0	0	0	0.95	1.0	1.0	0	1.0

struments Ltd., Bedfordshire, UK), and a Hanna HI 9142 temperature-compensated DO meter, respectively. Hyporheic and surface temperatures were observed to vary markedly among dates and locations (range 0.1–7.2 °C). DO measurements were therefore converted to percentage saturation, compensating for variations in temperature (and barometric pressure), to facilitate comparisons among sites and dates. Atmospheric pressure data were obtained from the meteorological synoptic station nearby in Aboyne (UK National Weather Service) (approximately 20 km east of the study site) and compensated for altitudinal change. The formula presented by Lee (1980) was used to derive saturation values for oxygen in water (O_2) at a given temperature and pressure. Thus,

$$O_2 = 14.6\, p/1000\, e^{-0.0247T}$$

where p is atmospheric pressure in millibars and T is water temperature in °C. Percentage saturation was calculated by dividing observed DO values by calculated saturation values.

Statistical approach

Each location was tested separately for depth-related effects on alevin weight using analysis of variance (ANOVA). Because the relationship between groundwater intrusion and depth is known to exhibit sharp discontinuities in some locations, depth was treated as a categorical rather than a continuous variable. P values were adjusted for the number of comparisons made using the Bonferroni method. Confidence intervals (95%) were calculated using the t distribution.

Alevin length was measured to the nearest millimetre. The distribution of lengths, therefore, comprised relatively few discrete values, and the use of ANOVA was considered inappropriate. Instead, each location was tested for an effect of depth on length using a randomisation (permutation) test (Manly 1997). The test statistic was the range of mean lengths (absolute difference between the smallest and largest means for all depths). The observed lengths were randomly reallocated to the observed depths (each depth retained the same number of observations) by resampling with replacement. The P value was derived as the number of replicates (of 999) with a test statistic greater than or equal to the test statistic for the observed data plus one (the observed data was included), divided by 2000 (the alternative hypothesis was directional). P values were adjusted for the number of comparisons using the Bonferroni method. Non-parametric bootstrapping with 1000 replicates was used to derive 95% empirical percentile confidence intervals (Dixon 2001).

Results

Embryo survival

On the date of excavation of the test arrays, all 347 ova retained in the control group had survived. Among eggs recovered from the stream, survival was zero in six of the most superficial groups (50 mm) among the 10 location arrays, but 100% in three other similarly placed groups (Table 1). Survival was zero in three of the deepest placed (300 mm) groups but 100%, or nearly so, in the others. Survival was total, or near total, in all intermediate groups with the exception of those at location 7. The most superficial group at location 7 (i.e., 7:50) was among those showing total survival, but in all deeper groups at this location, survival was zero (Table 1).

Assessment of embryo condition was not possible for those ova contained in the most superficial groups as partial degradation obscured any embryonic structure. At greater depths, dead eggs were denatured, but not degraded, so it was possible to discern the embryo and to categorise eggs according to the presence or absence (void) of a visible embryo and according to the state of embryonic development when mortality had occurred. At location 6, three embryos were present among 20 dead eggs recovered from 6:300. At location 7, a gradation of development stages at mortality was detected among groups 7:100 to 7:300. Group 7:100 contained 20 advanced ("eyed") embryos, 7:150, two "eyed" embryos plus 17 earlier stage embryos and a single void egg, 7:200, 16 embryos and four void eggs, 7:250, three embryos and 17 voids, and 7:300, two embryos and 18 voids. Elsewhere, single dead eggs were observed within incubation groups, none of which contained visible embryos.

Alevin condition at hatch

Retained ova, incubated in surface water, were examined at intervals to detect timing of and condition at hatch. None had hatched on 23 March, but 96% of all ova had hatched by 28 March. Among the remainder, delayed hatch was most marked among groups 6:250 and 9:300. First hatch in the former group was between 24 and 28 March and the last egg hatched between 3 and 6 April. In the latter group, first hatch was between 29 March and 2 April and last hatch was between 16 and 17 April.

All comparisons of alevin length (Table 2*a*) and most comparisons of alevin weight (Table 2*b*) showed significant variation within arrays. In seven of nine comparisons that could be made, mean body length was greatest at the shallowest burial depths at which embryos survived; groups

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Table 2. (*a*) Body length of alevins at hatch and (*b*) body weight of alevins (including yolk sac) at hatch.

(*a*) Body length of alevins at hatch.

	Location code number									
Incubation depth (mm)	2	3	4	6	7	9	10	12	13	16
50			20.8 (0.23)	19.9 (0.27)	20.7 (0.35)			21.0 (0.28)		
100	20.4 (0.29)	20.1 (0.41)	18.4 (0.41)	18.8 (0.31)		20.4 (0.31)	19.8 (0.37)	19.5 (0.48)	19.6 (0.46)	21.5 (0.27)
150	18.8 (0.48)	18.3 (0.52)	18.2 (0.44)	18.5 (0.42)		18.5 (0.80)	17.6 (0.52)	19.3 (0.63)	18.2 (0.52)	20.8 (0.60)
200	18.8 (0.37)	19.6 (0.41)	17.7 (0.41)	18.4 (0.48)		19.7 (0.46)	18.9 (0.42)	19.6 (0.30)	19.9 (0.59)	20.8 (0.48)
250	19.1 (0.36)	20.5 (0.51)	17.1 (0.50)	16.4 (0.38)		18.8 (0.47)	18.8 (0.45)	19.5 (0.36)	18.2 (0.67)	20.2 (0.41)
300	18.9 (0.50)	17.0 (0.56)	19.1 (0.49)			14.9 (0.43)	18.5 (0.41)	19.6 (0.39)		20.5 (0.46)
P	<0.005	<0.005	<0.005	<0.005		<0.005	<0.005	<0.005	<0.02	<0.02

(*b*) Body weight of alevins.

	Location code number									
Incubation depth (mm)	2	3	4	6	7	9	10	12	13	16
50			137 (1.6)	139 (1.1)	140 (1.7)			142 (1.8)		
100	140 (1.8)	136 (2.1)	133 (1.9)	135 (2.0)		137 (1.7)	140 (1.9)	136 (2.2)	139 (2.2)	141 (1.5)
150	135 (2.6)	133 (2.6)	134 (2.1)	136 (1.6)		136 (2.4)	132 (1.6)	136 (1.9)	134 (2.7)	138 (2.3)
200	137 (2.3)	135 (2.0)	133 (1.9)	135 (2.0)		136 (1.8)	134 (2.7)	140 (2.1)	137 (2.2)	138 (1.9)
250	137 (2.4)	138 (2.0)	130 (2.1)	134 (2.1)		133 (1.4)	134 (2.4)	141 (2.1)	134 (1.8)	137 (2.4)
300	133 (2.2)	129 (2.3)	134 (1.8)			133 (2.6)	135 (2.0)	138 (2.1)		139 (1.8)
P	<0.01	<0.05	<0.01	<0.01		<0.01	<0.05	NS	<0.05	NS

Note: The group means and 95% confidence intervals (in parentheses) are indicated. Significance levels for comparisons within locations are indicated. NS, not significant.

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Fig. 3. Mean alevin length (±95% confidence interval) for ova groups in relation to incubation depth. For clarity, groups have been arbitrarily split. Burial depths of some series have been offset for the same purpose.

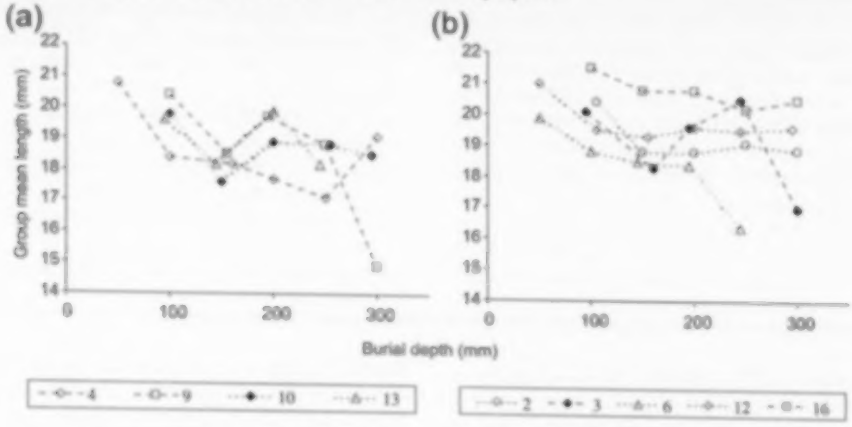


Fig. 4. Group means of alevin length in relation to group means for weight. The 95% confidence intervals for length are indicated. Two groups of outliers are identified.

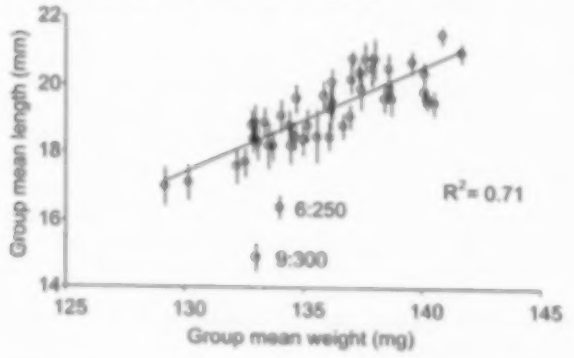
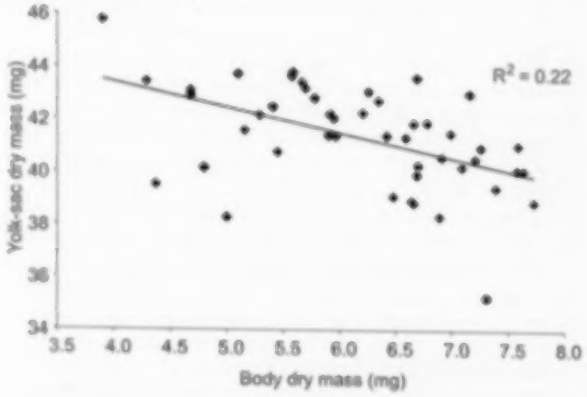


Fig. 5. The relationship between group mean values for dry body mass and yolk-sac dry mass.



3:250 and 13:200 were minor exceptions. Within arrays, there was a general tendency to reduced length with greater incubation depth, although considerable variation was evident and no single pattern was consistently expressed among arrays (Fig. 3).

In general, alevin weight and length were closely correlated (R^2 = 0.69 (excepting 6:250 and 9:300), $P < 0.001$; Fig. 4). Groups 6:250 and 9:300, which had delayed hatch times relative to the others, were notable exceptions and were treated as outliers. Group mean values for alevin length were significantly correlated with group mean values for dry body mass (R^2 = 0.64, $P < 0.001$). Group mean values for yolk-sac and body dry masses were inversely correlated (R^2 = 0.22; $P < 0.001$; Fig. 5). Yolk-sac dry mass varied from 35.3 (3:200) to 45.8 mg (6:250). Body dry mass varied from 3.90 (6:250) to 7.73 mg (2:250).

Oxygen saturation of hyporheic water

The spatial and temporal variability of oxygen saturation values in hyporheic water differed markedly among redd locations (Table 3). For example, saturation values were consistently high (>90%) at location 16, whereas low values (<30%) were a consistent feature of location 7. Overall, locations tended to rank consistently among sampling dates. Saturation values at location 4, however, were notably variable among sampling dates, the maximum detected saturation value exceeding the minimum value by 42%. In contrast, the corresponding difference for the most stable location (location 10) was 12%.

Mortality was a marked feature in deep incubation groups at locations 6, 7, and 13, which ranked 8th, 10th, and 7th, respectively, among all locations for both mean and minimum oxygen saturation values. However, mortality was absent at 4:300, which ranked 9th in both cases. Delayed hatch was a feature at 6:250 and 9:300. Location 6 ranked 8th for both mean and minimum values for oxygen saturation, but location 9 ranked among the higher quality sites at 2nd (mean oxygen saturation) and 4th (minimum value).

For the nine surviving groups at burial depths of 250 mm (the level corresponding to the mean sampling depth of hyporheic water), the group means for alevin length were strongly correlated with mean or minimum hyporheic oxygen saturation values (R^2 = 0.73 and 0.77, respectively, $P < 0.01$, in both cases; Fig. 6). At shallower depths, no significant correlation was evident. At the depth of 300 mm, only five groups survived and no correlation was evident.

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Table 3. Saturation of hyporheic water (%) by sampling date and location.

	Location									
Sampling date	2	3	4	6	7	9	10	12	13	16
17 November 2002	94	91	54	80	34	84	86	98	63	94
30 November 2002	84	84	47	69	19	91	85	84	72	88
12 December 2002	84	87	49	68	23	92	87	88	67	93
24 December 2002	85	89	67	64	26	95	93	88	81	92
09 January 2003	96	102	89	53	26	96	93	95	78	101
24 January 2003	81	89	51	67	30	91	91	91	67	92
09 February 2003	76	96	72	78	32	96	94	94	71	93
05 March 2003	91	104	59	78	38	103	97	96	74	99
Mean	86	93	61	70	28	94	91	92	72	94
Minimum	76	84	47	53	19	84	85	84	63	88

Fig. 6. Mean alevin length (±95% confidence intervals) for the nine surviving ova groups incubated at 250 mm below streambed level. The relationships between length and the mean (○) and minimum (◇) observed oxygen saturation levels are indicated.

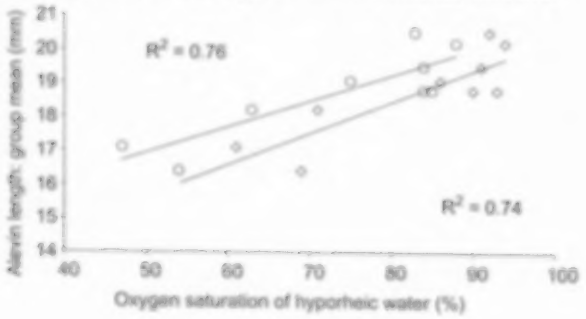
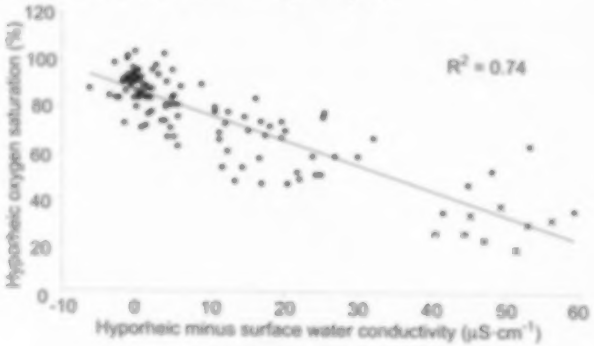


Fig. 7. The relationship between the conductivity of hyporheic water (expressed relative to surface water) and its oxygen saturation. Values for site 7 are indicated separately (×).



Conductivity of hyporheic water

Over all 15 sampling locations and dates, conductivity of hyporheic water was commonly greater than that of surface water, although small negative differences were also a feature of some comparisons (Fig. 7). Conductivity differentials between hyporheic and surface water were significantly and inversely correlated with hyporheic oxygen saturation (N = 15, R^2 = 0.75, P < 0.01). Large conductivity differentials (40–60 μS·cm^{-1}) were a consistently feature of site 7. However, the relationship was robust to exclusion of data derived from site 7, which the previous study had shown to be hydrochemically extreme (N = 14, R^2 = 0.60, P < 0.05).

Water temperature

Observed surface temperatures increased progressively over the course of each sampling day; values were generally greater in the lower altitude locations, which were consistently sampled later in the day. The greatest daily temperature range (2.3 °C) was observed on 5 March. The highest and lowest daily mean values were 6.4 °C (24 January) and 0.3 °C (9 January), respectively. Over the whole period of the experiment, the average value for surface water was 3.9 °C.

Hyporheic water temperature exceeded surface water temperature for 62 of the 80 paired measurements made. Over the whole period of the experiment, mean hyporheic temperature exceeded mean surface temperature at every location; the greatest difference was for location 7 (+1.9 °C) and the least for location 16 (+0.1 °C).

Discussion

The Girnock Burn represents a near-pristine hydrological environment. A catchment history of low-intensity agriculture and limited riparian forestry has ensured that only minor and superficial changes have been made to natural catchment flow paths. Spawning substrate is dominated by coarse sands and gravels; fine sediment content is low (Moir et al. 1998) and below the levels considered likely to result in substantial mortality of salmonid embryos (Chapman 1988). However, previous investigation at one of the locations examined in the present study (location 7) demonstrated high rates of mortality among salmon eggs associated with the presence of deoxygenated, long-residence groundwater (Malcolm et al. 2004).

In the present study, location 7 was again examined among an extended set of spatially representative spawning locations distributed throughout the catchment. Observed oxygen saturation values for hyporheic water were consistently lowest at location 7. Saturation was greatest at location 16 where hyporheic conditions had previously been shown to be dominated by well-oxygenated, downwelling stream water (Malcolm et al. 2002, 2003*a*). Over all sites, oxygen saturation of hyporheic water was inversely corre-

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lated with conductivity. Low oxygen and high conductivity are both characteristics of long-residence groundwater. High electrical conductivity results from the dissolution of mineral ions during passage through catchment substrates, and lowered oxygen (indicative of reducing conditions) is a result of the activity of anaerobic bacteria in subsurface sediment layers (Freeze and Cherry 1979). For the Girnock Burn, generally, the strong association of low hyporheic oxygen saturation with high hyporheic conductivity indicates that the variable intrusion of long-residence groundwater is the main determinant of oxygen levels at the depth range investigated.

Previous studies have demonstrated that exposure of incubating salmonid eggs to water depleted of oxygen results in mortality (Sowden and Power 1985; Rubin and Glimsater 1996; Malcolm et al. 2003*a*), an extended emergence period (Silver et al. 1963; Garside 1966; Hamor and Garside 1976), or retarded embryo development (Alderdice et al. 1958; Shumway et al. 1964; Rubin and Glimsater 1996). All of these phenomena were evident in the present study, and in general, each was associated with observed differences in the oxygen saturation of hyporheic water in the vicinity of the developing eggs, although notable exceptions and inconsistencies were evident.

At location 7, the findings of the present study are broadly consistent with previous findings in showing low levels of hyporheic oxygen and high levels of mortality over all incubation depths with the exception only of the most superficial group (Malcolm et al. 2004). The detection of embryos and the examination of the stage of development at which mortality had occurred showed a temporal gradation with depth, with earlier mortality at deeper incubation levels. This is consistent with the findings of Hamor and Garside (1976), who noted that low oxygen saturation of ambient water became more limiting on alevin development as development advanced.

Among the other sites, total mortality occurred in association with low hyporheic oxygen at two further locations (6 and 13), although survival was 100% in another (4) where observed oxygen values were similarly low. Delayed hatch was a feature of the deepest surviving groups at locations 6 and 9. Oxygen saturation values were relatively low at location 6 but consistently high at location 9. Equally, no delay was evident at location 4 where observed saturation values were lower than those at location 6. Within locations, embryo size generally declined with incubation depth, particularly at sites characterised by low hyporheic oxygen saturation values, although the patterns were again somewhat erratic.

This raises several possibilities. First, the sampling schedule may not have captured extreme events of high magnitude that occurred only at low frequency. Previous studies have shown that hyporheic conditions can be highly variable over time and that they change rapidly in response to hydrological events (Malcolm et al. 2003*b*, 2004). Second, hyporheic water samplers and incubation arrays were separated by between 0.5 and 1 m. Fine-scale spatial effects on groundwater intrusion (Malcolm et al. 2003*b*, 2004) may have resulted in discrepancies between the oxygen saturation values observed at the hyporheic sampling locations and the actual values in the vicinity of the test arrays. Finally, at the microscale (e.g., sampler size dimensions), intragravel velocities can be expected to vary. The design of the ova containers was intended to be consistent with natural intragravel porosities and is unlikely to have markedly affected the outcome of the experiment. However, variation in flow across ova groups will result where gravel composition, and even the position of individual clasts, generates preferential flow paths through the hyporheic sediments. Such effects might operate at scales relevant to the ova containers without being apparent at the operational scale associated with sampling.

Low through-flow is likely to impose two related effects on developing ova. On the one hand, the delivery of oxygen mass, particularly by unsaturated water, may become critically low and oxygen utilisation by embryos may reduce oxygen saturation values in their immediate vicinity. Additionally, interstitial flow appears to be necessary for removal of toxic metabolic products, as experimental studies have shown that interstitial velocity can affect development independently of dissolved oxygen concentrations (Shumway et al. 1964; Hamor and Garside 1976; Sowden and Power 1985). Such effects may explain some of the subtler in-site variation in body size, as evident in this study. A general discontinuity in body size between groups incubated at 150 mm and above and those incubated at greater depths is also evident. When the test arrays were recovered from the stream, it was noted that coarse sand had typically infiltrated the upper but not the lower ova containers, as would be expected where coarse material infiltrates streambed sediments (Lisle 1989). Infiltration could not be quantified because sediment was lost as the containers drained during recovery from the streambed. Gravel infiltration after the installation of the test arrays (as for the case of natural redds) may have impeded local flow pathways to some of the upper ova groups in the test arrays.

Although the causes of these unexplained variations will require further investigation, the main findings of the study appear to be clearly established. Hyporheic oxygen levels varied among sites and were inversely correlated with conductivity values. The strength of the relationship indicates that the local intrusion of long-residence, deoxygenated groundwater was the main determinant of variations in oxygen levels in hyporheic water at the sampled depth (200–300 mm). For the most relevant test depth (250 mm), mean alevin size was correlated with the average oxygen level observed in hyporheic water. Together, these relationships link embryo performance to the hydrology of the hyporheic mixing zone, and in particular, they identify groundwater intrusion as a constraint on embryo performance. Reduced performance with depth was not attributable to the possible effects of low incubation temperature on development rate, as hyporheic (i.e., deeper) water tended to be warmer than surface (i.e., shallower) water. Links between groundwater intrusion and embryo performance were demonstrated for non-lethal effects on growth, but by extension, it appears plausible that the same effects extend to include the high mortality rates observed in some egg groups at the deeper burial depths.

On the other hand, mortality was a particularly marked feature of the shallowest set (50 mm) of egg groups. This was probably the result of physical disturbance, perhaps through undetected turnover of the superficial layers of the streambed during high flow events. Considered together, these observations partly identify the dilemma faced by spawners

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in relation to egg burial depth and progeny survival. In addition, however, alevins tended to be smaller at greater depths, even at locations showing good hyporheic environmental quality (mean saturation values >90%). These differences extended to variations in body dry mass, and at hatch time, the mean value for the heaviest incubation group exceeded the value for the lightest group by a factor of about two. However, smaller alevins showed a reciprocally greater dry weight of residual yolk mass than larger ones, suggesting that small alevin size was probably attributable to retarded, rather than less efficient, conversion of yolk material.

Size at emergence (Einum and Fleming 2000) and time of emergence (Mason and Chapman 1965; Chandler and Bjorn 1988) are determinants of fitness. Variation in one or both is likely to follow from impaired conversion of yolk mass to somatic tissue. The potentially critical effects of female spawning behaviour on egg burial depth, and therefore progeny fitness, can be seen to operate on a very fine scale when these effects are considered. Additionally, the hyporheic environmental quality varies spatially on grosser scales, and when the effect of the females' choices of nest site on the mortality and development of progeny is also considered, the potential complexity of the origins of successive generations becomes apparent. For individuals, a risk-spreading strategy would counter effects associated with particular sites. Indeed, in the Girnock Burn, female salmon spread their ova among several locations in repeated bouts of spawning; males distribute spawning activity in an equivalent way (Taggart et al. 2001).

From a management viewpoint, targeted hydrochemical measurements made in areas of streams of potential interest can identify long-residence groundwater intrusion, although fine-scale spatial heterogeneity is likely to make generalisation problematic. In this regard, less direct approaches may be possible for identifying likely areas of interest, at reach or catchment scales, based on catchment topography, geology, and geomorphology.

No latitude appears to exist for ameliorating hyporheic environmental conditions in a pristine stream like the Girnock Burn. Hatchery practice can be used to obviate any constraints on fry recruitment associated with low hyporheic quality but it is only likely to prove worthwhile in extremis, when spawner numbers, egg deposition, and recruitment are low. More generally, however, the effects observed in this study were marked and probably important, and they were generated in a near-pristine catchment with intact natural hydrological pathways. The frequency and severity of effects on ova survival and development are probably greater in catchments where hydrological pathways have been modified. For example, Dahm et al. (1998) suggest that canalisation disconnects the surface water – groundwater interface by speeding the flow of surface water and reducing interactions between the stream channel and the hyporheic and riparian zones. In addition, canalisation creates uniform drainage channels that are devoid of the natural geomorphological variability that drives hyporheic exchange between the stream channel and its bed (e.g., Vaux 1968). This effect is likely to be exacerbated where land-use practice results in the delivery of high loads of fine sediment to streams (Soulsby et al. 2001). All of these effects are likely to increase the dominance of groundwater at shallow depths in the hyporheic zone. Long-residence groundwater impacts should therefore be added to the list of environmental factors to be considered as potential determinants of production in salmonid streams.

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Long-term consequences of variation in timing and manner of fry introduction on juvenile Atlantic salmon (*Salmo salar*) growth, survival, and life-history expression[1]

Benjamin H. Letcher, Todd Dubreuil, Matthew J. O'Donnell, Mariska Obedzinski, Kitty Griswold, and Keith H. Nislow

Abstract: We tested the influence of introduction time and the manner of introduction on growth, survival, and life-history expression of Atlantic salmon (*Salmo salar*). Introduction treatments included three fry stocking times and stream rearing of embryos. Despite poor growth conditions during the early stocking period, early-stocked fish were larger throughout the entire study period, likely the result of prior residence advantage. This interpretation was reinforced by the laboratory study, where early-stocked fish outgrew late-stocked fish when reared together, but not when they were reared separately. In contrast to growth, abundance of stocked fish was greatest for fish stocked during the middle period, and this stocking group produced the greatest number of smolts. Despite smaller size, survival of stream-incubated fish was generally greater than survival of stocked fish. Introduction timing had a pronounced effect on smolt age but a weak effect on extent of parr maturation. Overall, these observations indicate that small differences (~2 weeks) in introduction time can have long-term effects on size, survival, and life-history expression. Results suggest stabilizing selection on introduction times, mediated by the interaction between prior residence (advantage to fish introduced earlier) and habitat suitability (advantage to fish introduced later).

Résumé : Nous avons évalué l'influence du moment et de la méthode d'empoissonnement sur la croissance, la survie et le déroulement du cycle biologique chez le saumon atlantique (*Salmo salar*). Les méthodes d'empoissonnement comprenaient des ensemencements d'alevins à trois périodes différentes, ainsi que l'élevage d'embryons dans le cours d'eau. Malgré les mauvaises conditions de croissance durant les périodes hâtives d'empoissonnement, les poissons introduits tôt étaient plus grands durant toute la période de l'étude, sans doute le résultat de l'avantage d'une occupation précoce. Cette interprétation se trouve renforcée par une étude de laboratoire qui montre que les poissons ensemencés tôt croissent plus rapidement que des poissons ensemencés tard lorsqu'ils sont élevés ensemble, mais non quand ils sont gardés séparément. Contrairement à la croissance, l'abondance des poissons introduits est maximale pour les empoissonnements de mi-période et c'est dans ces conditions que le nombre maximal de saumoneaux est produit. Malgré leur taille réduite, les poissons incubés dans le cours d'eau survivent généralement mieux que les poissons ensemencés. Le moment de l'empoissonnement a un effet marqué sur l'âge des saumoneaux, mais un effet faible sur l'importance de la maturation des tacons. Dans leur ensemble, nos résultats indiquent que de petites différences (~2 semaines) dans le moment de l'empoissonnement peuvent avoir des effets à long terme sur la taille, la survive et le déroulement du cycle biologique. Les résultats indiquent l'existence d'une sélection stabilisante des temps d'empoissonnement, effectuée par l'interaction entre l'occupation précoce (avantageuse au poisson introduit tôt) et la valeur de l'habitat (avantageuse au poisson introduit plus tard).

[Traduit par la Rédaction]

Introduction

The transition from endogenous to exogenous feeding in stream-dwelling salmonids involves major shifts in energetic strategies, habitat requirements, and mortality risks. Not surprisingly, mortality during this life-history stage can be very high, and these high mortality rates may significantly influence population dynamics and cohort strength (Elliott 1989;

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B.H. Letcher,[2] T. Dubreuil, M.J. O'Donnell, M. Obedzinski, and K. Griswold. S.O. Conte Anadromous Fish Research Center, USGS/Leetown Science Center, Turners Falls, MA 01376, USA.
K.H. Nislow. Northeastern Research Station, US Forest Service, University of Massachusetts, Amherst, MA 01003-9285, USA.

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[2]Corresponding author (e-mail: bletcher@forwild.umass.edu).

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Jensen and Johnsen 1999). Because of the highly dynamic seasonal nature of most north temperate stream environments, the ability of newly emerged juveniles to survive and grow may be strongly influenced by the time at which they emerge. These influences can then exert significant selective pressure on emergence timing in populations. For example, Jensen et al. (1991) found that in a large-scale survey of Norwegian streams, median Atlantic salmon (*Salmo salar*) emergence time occurred either before or after, but not during, the typical occurrence of peak spring flows that would likely result in catastrophic displacement of newly emerged fry. Similarly, delayed fry emergence times in high- vs. low-altitude tributaries in the catchment of the Aberdeenshire Dee in Scotland were interpreted by Webb and McLay (1996) to be adaptive in the context of optimal fry survival in different parts of the river system. The results of these studies suggest that natural emergence patterns might be timed to maximize juvenile growth and survival in natural populations of migratory Atlantic salmon.

These issues are particularly significant given range-wide declines in the populations of anadromous Atlantic salmon. Populations that have been extirpated or are in immediate danger of extirpation are increasingly being restored or supplemented by stocking programs (e.g., Kennedy 1988; Moring et al. 1995; Schramm and Piper 1995). Stocking of unfed fry, when they are ready to begin feeding, is frequently a preferred hatchery supplementation method. If stocking occurs when environmental conditions are unfavorable for growth and survival, major efforts could be wasted and loss of a cohort could result. In addition to implications for stocking strategy, anthropogenic alteration of river hydrologic regimes, caused by river regulation (Poff et al. 1997) or global climate change (Meyer et al. 1999), may seriously disrupt the relationship between stocking, emergence, and salmon performance.

The relationship between timing of emergence and juvenile performance is likely determined by a complex interaction of biotic and abiotic factors. Salmonids in north temperate streams typically emerge in spring, a time of year characterized by major changes in physical conditions as streams change from the high flows and cold temperatures of spring runoff to warmer and lower flows characteristic of summer conditions (Poff and Huryn 1998). Early-emerging individuals may therefore experience harsher environmental conditions (higher flows, colder temperatures) than later-emerging individuals (Nislow et al. 2000) but may benefit from effects of prior residence (Cutts et al. 1999; O'Connor et al. 2000) and a longer growing season. Previous studies have demonstrated significant positive effects of early emergence, likely associated with prior residence (Cutts et al. 1999; Einum and Fleming 2000), although Brannas (1995) found that increased exposure to predators diminished advantages for early emergers. By manipulating fertilization times within sib-ships and following individuals, Einum and Fleming (2000) found that early-emerging fry had higher survival and growth rates and demonstrated clear selection for early emergence in an Atlantic salmon population in Norway. However, they did not follow juveniles past their first summer (<4 months after emergence). Given the possibility of compensatory growth (Metcalfe and Monaghan 2001) and the potential interactions between growth, survival, and maturation (Metcalfe 1998; Letcher and Gries 2003), it is unclear how these early differences will ultimately manifest in growth and survival differences over the entire duration of stream residence and how they will ultimately affect life-history expression and smolt production.

In this study, we tested the influence of introduction time and the manner of introduction (stocking or stream rearing) on growth, survival, and life-history expression of Atlantic salmon using a combination of field and laboratory studies. We stocked unfed fry into a long-term study site at three different stocking times while simultaneously incubating eggs within the stream. We then measured the survival, growth, and maturation of the four treatment groups in repeated samples from the summer after stocking/emergence through smolt outmigration, keeping track of treatment groups using a combination of genetic batch marks and individual passive integrated transponder (PIT) tags. At the same time, we conducted a laboratory study, using subsets of the same groups of fish, to test for effects of prior residence on growth differences between early- and late-stocked groups. Our goal was to use variation in stocking time and stream introduction method (natural emergence vs. stocking) to test the long-term consequences of variation in early experience on juvenile stream-dwelling Atlantic salmon.

Materials and methods

Study site

The experiment was conducted in the West Brook, Massachusetts, USA (42°25′N, 72°39′W), a third-order tributary in the Connecticut River basin. Average wetted width of the study area was 4.7 m, average depth was 8.8 cm, average gradient was 2%, and average substrate size was 21.5 cm (details in Letcher et al. 2002). The ~1-km study site was divided into 47 contiguous 20-m sections with an average area of 96.6 m^2-section^{-1}. Atlantic salmon, brook trout (*Salvelinus fontinalis*), and brown trout (*Salmo trutta*) were the only fish species present in the study site. Brook and brown trout reproduce naturally, whereas all salmon present have been stocked (unfed fry). Salmon fry have been stocked into the West Brook for at least the last 10 years.

Temperature and water depth were measured every 2 h using a data sonde (model 600XLM-SV; YSI Inc., Yellow Springs, Ohio). Depth was converted to stream flow using a stage (depth) – discharge relationship determined by estimating stream flow and depth across a range of flows ($N = 198$, $r^2 = 0.87$). Daily rainfall (mm·day^{-1}) was measured with a rain gauge (Davis Rain Collector II; Davis Instruments Corp., Hayward, Calif.) equipped with a data logger (Onset HOBO® Event Logger; Onset Computer Corp., Pocasset, Mass.).

Source of fish

Each spring, except for the year class in this experiment (2001 cohort), unfed Atlantic salmon fry (26- to 28-mm fork length; White River National Fish Hatchery, US Fish and Wildlife Service, Bethel, Vermont) have been stocked throughout the West Brook at a density of 50 fry/100 m^2. Most (~80%, depending on year) fish smolt at age 2+ and a large proportion of males mature at age 1+ (Letcher and Gries 2003).

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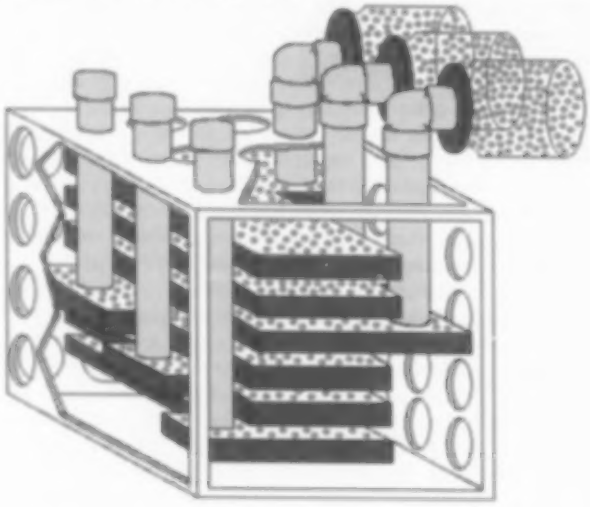
To assess the relative growth, survival, and life-history expression of fish stocked at one of three stocking times or incubated in-stream (hereafter collectively called introduction groups), we divided eggs from 10 sea-run origin mothers (all 2-sea-winter fish) into four lots. Each lot was then fertilized with milt from 1 of 40 randomly chosen fathers (8 sea-run and 32 mature parr) so that eggs from each female were fertilized with milt from four males. Male parr maturation rates are very high (80%–100%) in the Connecticut River (Letcher and Gries 2003), so most sea-run males had probably been mature as parr. To equalize maternal contribution across introduction groups, we randomly selected one lot from each mother for each introduction group, except for the incubator group, which received lots from five mothers instead of 10 (owing to limited space in the incubator). Because lots had unique parent pairs, fish could easily be identified using parentage assignment with known matings and multilocus microsatellite genotypes (Chakraborty et al. 1988; Bernatchez and Duchesne 2000; Letcher and King 2001) following release. We used five loci (SSA197, SSA202, SSA171, SSA85 (O'Reilly et al. 1996), and SSOSL85 (Slettan et al. 1995)) to characterize parentage. Fish with unknown parentage were stocked outside of the study site at the same time as the middle stocking group at a density of 50 fry/100 m^2. There were no barriers precluding movement in or out of the study site.

Eggs for the stocking groups were fertilized on 16 and 23 October 2000 and eggs for the in-stream incubator group were fertilized on 30 October 2000. Fertilized eggs for the incubator group were transferred to in-stream incubation trays on the day of fertilization. Fertilized eggs from the remaining lots were brought to the White River National Fish Hatchery and were reared there until egg eyeing, at which point they were transferred to the Conte Anadromous Fish Research Center for rearing until stocking. To account for variation in the timing of fertilization and to achieve target developmental stages for stocking, development rates were adjusted by varying temperature within the first 2 months following eyeing so that all fish from a single stocking time reached a "developmental index" (Kane 1988; Letcher and Terrick 2001) of 92 by the time of stocking. A target developmental index of 92 is used for the majority of fish stocked in the Connecticut River basin and represents 92% of the development towards exhaustion of yolk reserves.

In-stream incubator box

The incubation box (Fig. 1) was modeled after boxes described in Donaghy and Verspoor (2000). The overall box dimensions were 34.3 cm height × 27.0 cm width × 33.0 cm length. A hole in the stream bottom was fitted with a sleeve constructed from expanded and flattened 1.9-cm steel mesh. During incubation, the box was placed in the sleeve. Following placement of the box in the sleeve, the box was covered with a lid of more steel mesh and rocks. Embryos from each family were housed in separate trays (volume of each tray was 140.8 cm^3), and each tray was removable from the box. Trays had lids made of perforated plastic that retained embryos and alevins but allowed water to flow through. The lids were removable and could be replaced with new lids designed with a hole to receive a tube that led to a collection jar. These characteristics allowed periodic checking of survival of embryos and alevins from each family. We checked embryo and alevin numbers on 7 March and 4 May and determined the maximum number of fry available to emerge from each family. In an attempt to release known numbers of fry from each family upon emergence, each tray was fitted with an emergence tube and cap on 4 May. Two weeks before anticipated emergence (based on temperature-dependent development rate (Kane 1988)), caps were replaced with fry emergence traps (Fig. 1) and the traps were checked each morning and evening. Our goal was to release equal numbers (100) of emerging fry per family; actual numbers exceeded the target of 500 owing to unintended releases. Emerged fry were released in the morning immediately downstream of the incubation box. The incubation box was located 300 m downstream from the top of the study site.

Fig. 1. Cut-away drawing of the in-stream incubator box. The box contained six independent trays, each fitted with an emergence tube. The three tubes on the left are shown capped (between last trap check and 2 weeks before emergence). The three tubes on the right are shown with attached emergence traps (replaced caps 2 weeks before emergence). The box was buried in the substrate to a level slightly below the caps.



Stocking times

Fry were stocked using standard scatter-stock methods from black buckets during the day at three stocking times (Table 1). Times were separated by about 2.5 weeks and the middle stocking corresponded with the typical date of stocking for the stream (last 10 years). For each stocking time, fry from each of the 10 families were mixed together before stocking and were spread evenly throughout the study site.

Stream temperatures and flows varied across stocking times (Fig. 2). Temperature was cold and flows were high for the early stocking, values were intermediate for the middle stocking, and temperature was slightly higher during the late stocking than during the middle stocking, but flows were lower (Table 1). Shortly after the late stocking, flows briefly increased to ~1 $m^3 \cdot s^{-1}$ in response to rainfall and then continued to decline.

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Table 1. Introduction date, environmental conditions, and numbers of families and numbers released for each group.

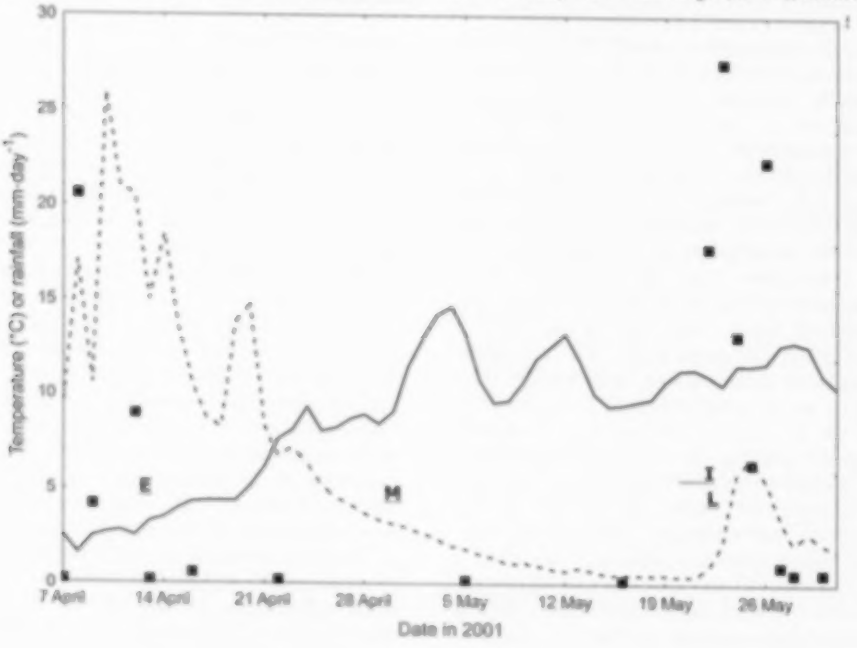
Introduction group	Date	Water temperature (°C)	Average discharge ($m^3 \cdot s^{-1}$)		No. of families	Total no. released
			On day of stocking	Over 7 days after stocking		
Early	13 April	3	2.50	2.09	10	1500
Middle	30 April	9	0.52	0.35	10	1500
Late	22 May	11	0.15	0.68	10	1500
Incubator	18–25 May	11	0.41	0.64	5	725

Note: Emergence for the incubator group occurred over a range of dates.

Table 2. Sampling dates and techniques for each sample.

Sampling age and description	Sample no.	Starting date	End date	Median date
Age 0+ summer	35	20 July 2001	6 Aug. 2001	28 July 2001
Age 0+ fall	36	4 Sept. 2001	3 Oct. 2001	18 Sept. 2001
Age 0+ winter	37	3 Dec. 2001	11 Dec. 2001	7 Dec. 2001
Age 1+ presmolt	38	25 Mar. 2002	10 Apr. 2002	2 Apr. 2002
Age 1+ postsmolt	40	6 June 2002	2 July 2002	19 June 2002
Age 1+ fall	41	17 Sept. 2002	31 Oct. 2002	9 Oct. 2002
Age 2+ presmolt	43	2 Apr. 2003	21 Apr. 2003	11 Apr. 2003
Age 2+ smolt	44	21 Apr. 2003	2 June 2003	12 May 2003
Age 2+ postsmolt	45	10 June 2003	24 June 2003	16 June 2003

Fig. 2. Environmental conditions during early (E), middle (M), late (L), and incubator (I) introductions. Length of underline indicates duration of introduction (fry release). Temperature (°C), solid line; rainfall ($mm \cdot day^{-1}$), ■; discharge ($m^3 \cdot s^{-1}$), broken line.



Sampling

Fish were captured in the stream using standard electrofishing techniques and with a smolt trap (modified screw trap) as they were emigrating (Table 2; sample numbers are presented to retain consistency with other published papers, the missing sample 39 was a smolt trap sample for older fish). Fish were first caught in summer (age 0+) when they were big enough to tag with 11-mm PIT tags (Digital Angel Corp., St. Paul, Minnesota). Subsequent samples were conducted in winter (age 0+), spring, early summer, and autumn (age 1+), and in spring, late spring, and early summer (age 2+). There was no winter age-1+ sampling (sample 42) because ice cover prevented electrofishing. Sampling con-

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sisted of sequentially collecting fish in the 47 study sections from downstream to upstream. Before sampling, each section was isolated using block nets (9-mm mesh). We conducted two electrofishing passes (400- to 500-V unpulsed DC) in each section, placing small weighted flags on the stream bank to indicate capture location. After fish recovery, individuals were replaced in the approximate stream locations indicated by the flags. Although we collected data on specific locations of each fish, for the analysis reported here, data have been pooled over all sampling locations within the study site.

After capture, individuals were anesthetized (MS-222), weighed (±0.01 g), measured (±1 mm), tagged if they were untagged, scale sampled for age determination, anal fin clipped for genotyping, and digitally photographed. Mature male parr were identified by the expression of milt following gentle pressure on the abdomen. PIT tags were inserted intraperitoneally through a small incision made with a scalpel between the pectoral fins. Tag retention (>99%) and survival (95%) were both high using this technique (Gries and Letcher 2002). We tagged fish that were >60 mm and >2 g wet weight. All data were recorded using field computers (Juniper Systems, Logan, Utah).

Fin clips were placed in absolute ethyl alcohol and kept chilled for 24 h. DNA extracted from the fins was amplified using standard polymerase chain reaction (PCR) techniques, and allele values were determined with Applied Biosystems sequencers (Applied Biosystems, Foster City, Calif.). Genotyping details are in Letcher and King (2001).

To capture emigrating smolts, we installed a smolt trap approximately 3 km downstream of our study site. The trap was a combination of a rotary screw trap and resistance board panels placed on both sides of the screw trap. We placed bulkheads on either side of the panels, and picket weir fences extended from the outside wall on each panel to the stream bank. Because the screw did not rotate and therefore catch fish under low flow conditions, we placed a fyke net behind one of the picket weirs. When flows were low, we raised 10–20 of the pickets in front of the fyke net so that fish could pass through the fence and into the net. The smolt trap was operated from 21 April to 2 June 2003.

We also installed a PIT tag antenna weir 200 m upstream of the smolt trap as a check on possible inefficiencies of the smolt trap. The weir was a standard picket weir (Anderson and McDonald 1978), but instead of a fish trap, we placed a PIT tag antenna in the notch of the V created by the weir. The antenna was connected to a PIT tag reader (FS-1001; Digital Angel Corporation), which decoded the PIT tag numbers. Time/date and PIT tag number data were stored on a personal computer using Minimon software (available as MinimonSetup.exe at http://www.psmfc.org/pittag/Software_and_Documentation/index.html). Antenna efficiency tests indicated that read efficiency was high (>95%) but that more than one fish passing through the antenna at the same time could reduce efficiency resulting from tag interference.

Laboratory growth study

To evaluate the growth implications of interactions between fish from different stocking times, we conducted a laboratory study in which early and late fish were grown in either the same or separate tanks. On the same day as the early and late stockings (Table 1), randomly sampled fish from the pool of stocked fish were placed into one of two replicated tanks from one of three treatment groups. The three groups resulted in four actual treatments: early alone, late alone, early mixed with late, and late mixed with early. Fish densities were adjusted so that alone and mixed treatment tanks contained the same number of fish once the late fish were added to tanks; 144 fish were placed in tanks from each of the alone treatments and 144/2 fish from each stocking time were placed into the mixed treatment tanks. Before late fish were added to the mixed tanks, food densities in the early mixed tanks were one-half those of the early alone tanks. After addition of the late fish, fish in all tanks were fed ad libitum (overfed the same amount) three times per day. Treatment identity of fish in the mixed tanks was determined with a calcein mark (Mohler et al. 2002) on the late fish. Calcein marks were clearly evident under ultraviolet (UV) light throughout the course of the experiment. Mohler et al. (2002) found no effect of the marking procedure on growth or survival of Atlantic salmon. Fish were fed a mixture of dry fish food and *Artemia* nauplii. Tank temperatures and photoperiod were adjusted to mimic stream conditions. In each tank, masses of 20 randomly selected individuals from each stock time were measured six times total (early May to early October) for the early fish and five times (late May to early October) for the late fish.

Data analysis

Abundance/survival

We used Cormack–Jolly–Seber (CJS) mark–recapture models in program MARK (White and Burnham 1999) to determine whether survival varied among introduction groups from the time of tagging to smolting. Using program RELEASE within MARK, we first ran goodness-of-fit tests to determine whether the CJS model described the data well and to evaluate violations of the primary assumptions of the CJS model (equal survival and catchability among fish). We report P values and $\hat{c}$ values for each group for the combined TEST 2 + TEST 3 result within RELEASE. P values less than 0.05 indicate significant violation of the assumptions, and $\hat{c}$ values provide a measure of model overdispersion (Burnham and Anderson 1998).

In the context of MARK, hypotheses are tested by making comparisons of models of varying complexity using Akaike's information criterion (AIC_c; Burnham and Anderson 1998). By combining model log-likelihood and the number of parameters, AIC_c orders candidate models along a parsimony gradient. The importance of group and time effects can be evaluated by comparing relative weights (AIC_c) of models that include parameter estimates for groups or times with models that do not. For example, group effects would be considered important if a model including group effects had higher AIC_c weights than models that did not.

To test for introduction group effects, we ran a set of candidate models that included all possible combinations (16 models total) of group and no group for both probability of apparent survival (ϕ) and capture (p). Model notation follows Lebreton et al. (1992), where group (G) and time (t) effects are specified in parentheses following ϕ or p. An asterisk (*) signifies no effect in the model. For example, a $\phi(G, *), p(*, t)$

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Table 3. Numbers of fish captured from each introduction group, numbers tagged and not tagged (fish that were too small to tag or untagged in smolt trap), total number of fish captured, and proportion of fish that were recaptured (tagged in previous samples). Also shown is the proportion of fish captured but not assigned to one of the introduction groups (immigrated from outside study site) and the proportion of genotyped fish that were not assigned to one of the introduction groups.

	Introduction group									
Sampling age and description	Early	Middle	Late	Incubator	No. tagged	No. not tagged	Total no. captured	Proportion recaptures	Captured but unassigned	Proportion unassigned of genotyped
Age 0+ summer	37	73	—	—	121	204	325	0	9	0.08
Age 0+ fall	67	196	44	35	411	143	554	0.19	66	0.16
Age 0+ winter	50	163	48	47	363	71	434	0.60	53	0.15
Age 1+ presmolt	37	114	40	68	355	31	386	0.63	81	0.24
Age 1+ postsmolt	38	108	37	60	311	0	311	1.00	60	0.20
Age 1+ fall	33	87	34	53	262	0	262	0.98	51	0.20
Age 2+ presmolt	10	26	13	30	97	0	97	1.00	18	0.19
Age 2+ smolt	11	17	7	5	48	21	69	0.70	29	0.48
Age 2+ postsmolt	6	18	12	28	77	0	77	1.00	13	0.17

model contains group effects but no time effect in ϕ, and no group but a time effect in p. In addition to models that included interactions between group and time, we ran an additive survival model that allowed additive variation only (no interaction) among groups over time ($\phi(G + t)$). We then compared model weights among candidate models to assess if probabilities of capture and survival varied with time or introduction group. Based on results from the first set of runs, we also evaluated whether survival of introduction groups varied by comparing models that included separate parameter estimates for all possible combinations of groups.

When relatively high AIC_c weights (>0.25) are distributed across several candidate models, model averaging should be used to derive weighted parameter estimates that account for model selection uncertainty (Burnham and Anderson 1998). Model averaging in MARK weights parameter estimates from each model by the AIC_c weight. To obtain survival estimates and confidence intervals for groups based on unconditional standard errors, we conducted model averaging for the set of models comparing survival among groups.

In the CJS analysis described so far, survival estimates are possible only while fish were tagged. Because early mortality before tagging could influence abundances and because the incubation group had lower initial numbers of fish (Table 1), we also estimated abundances of the different groups using a variant of the CJS model (Jolly–Seber model). We used this model with group effects to generate abundance estimates with a time-varying model. We then scaled estimated abundances to numbers of fish released into the stream from the different introduction groups to provide an estimate of proportion of released fish that survived to various samples. Unfortunately, this approach is not good for hypothesis testing because of the extra parameters that must be estimated in the Jolly–Seber model, but it does provide a rough estimate of survival from fry introduction to each sample.

Size/growth

Masses of fish from the introduction groups were compared using a two-way analysis of variance (ANOVA) with group and sample as the independent variables. To evaluate mass difference among groups at specific samples, we also ran one-way ANOVAs with mass as the dependent variable and group as the independent variable. Because we could separate earlier masses of tagged individuals based on whether they smolted or not, we also evaluated mass differences among groups across samples for fish that either smolted or did not using ANOVA followed by linear contrasts among groups.

Growth of individuals caught on consecutive samples was also compared among introduction groups. We did not use standard instantaneous growth rates to compare growth of fish from different groups because this method of estimating growth is sensitive to differences in initial size. Preliminary analysis demonstrated variation in size among groups in all samples. Instead, we used analysis of covariance (ANCOVA) with final size (size at the end of an interval) as the dependent variable, introduction group as the categorical grouping variable, and initial size (size at the beginning of an interval) as the covariate. We first tested for homogeneity of slopes among groups. If slopes were not different, then we removed the interaction term for the ANCOVA to test for differences in final size after accounting for variation in initial size. Sample size was insufficient for a growth estimate from the age-2+ presmolt to the smolt trap sample.

We analyzed mass data from the last sample of the laboratory growth study using a one-way ANOVA with the four treatments (early/alone, late/alone, early/mixed, late/mixed) as the independent variable and mass as the dependent variable. We ran a Tukey's honest significant difference post-hoc test to examine pairwise treatment differences in mass.

Results

Overall, 98.7% of the fish tagged were genotyped. Of these, 76% to 92% were assigned to families from one of the introduction groups depending on sample number (Table 3). Two hundred and four fish were too small to tag during the age-0+ summer sample; this number dropped to 31 by the age-1+ presmolt sample and was zero for subsequent samples before the smolt trap (Table 3). In the second sample (age 0+ fall), 19% of the fish had been tagged in the previous sample (age 0+ summer). Thereafter, proportion recap-

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Table 4. Goodness-of-fit test (test 2 + test 3 within program RELEASE) for the Cormack–Jolly–Seber mark–recapture model for the four introduction groups.

Introduction group	χ^2	df	$\hat{c}$	*P* level
Early	1.93	10	0.19	0.99
Middle	9.032	10	0.90	0.53
Late	0.26	7	0.037	0.99
Incubator	4.22	7	0.60	0.75
Total	15.44	34	0.45	0.99

tures increased and reached 100% by the age-1+ postsmolt sample (Table 3).

Survival/abundance

Goodness-of-fit tests indicated that the CJS model provided a good description of the data and that the major assumptions of equal capture and survival probabilities for tagged and untagged fish were not violated (all *P* values > 0.05 and $\hat{c} < 1$; Table 4). Values reported in Table 4 summarize the combined tests 2 and 3 from program RELEASE. There were no violations of goodness-of-fit assumptions for any of the specific tests within tests 2 and 3 for any introduction group.

For probability of capture, all models with AIC_c weights greater than 0.001 contained no group effect but a time effect (Table 5), indicating that probability of capture did not vary among groups but did vary with time. Therefore, subsequent models estimated probability of capture using a $p(*, t)$ model.

Probability of survival varied among groups and there was some evidence for time variation. The model receiving the most support (AIC_c weight 0.79) included a group effect but no time effect, whereas the second-ranking model (AIC_c weight 0.12) did not include group effects and did include time effects. The final model with AIC_c weight > 0.001 (0.09) contained neither group nor time effects (Table 5). Both the model containing group and time interactions ($\phi(G, t)$) and the additive model received no support ($AIC_c = 0$). Taken together, these results suggest that the data are not sufficiently structured in both group and time effects to accommodate the high number of parameters required for models containing both group and time effects. Separately, group effects appear to account for over sixfold more variation in survival than did time effects. Overall, model-averaged sample-to-sample survival (confidence interval, CI) was higher for the incubator (0.71; CI = 0.64–0.77) and late (0.70; CI = 0.61–0.77) groups than for the early (0.63; CI = 0.56–0.69) and middle (0.61; CI = 0.56–0.65) groups.

An additional set of models (all with p(*, t)) testing survival of specific group combinations reinforced the observation that group differences in survival were important and indicated that survival of the incubator (I) and late (L) groups was similar and different from the early (E) and middle (M) groups (model E = M, L = I) (Table 6). Models with either late and (or) incubator groups from other groups separately garnered considerably more support (combined AIC_c weights of 0.84) compared with the model with simple group variation (model E, M, L, I, AIC_c weight = 0.10), indicating that variation in survival between the late/incubator and early/middle groups was highly structured (i.e., not equally spread across groups).

In addition to differences in survival, there were marked differences in abundance estimates scaled to numbers of introduced fry among introduction groups over time (Fig. 3). Early in the sampling when only fish from the early and middle introductions were large enough to tag, abundances of the middle fish were over threefold higher than abundances of early fish. Abundances of late fish were similar to those of early fish (Fig. 3). Abundances of incubator fish, although they entered the stream at approximately the same time as the late fish (Fig. 2), were similar to or higher than those of the middle fish and twofold higher than those of the late fish (Fig. 3). Unfortunately, mark–recapture models in the CJS class cannot estimate abundances effectively for the last sample, but it appears, based on simple counts of fish captured (Table 3), that numbers of incubator fish were decreasing less rapidly between age-1+ fall and age-2+ presmolt samples than middle fish, and therefore, incubator abundance may actually be greater than middle group abundance by age 2+ in the spring.

Size/growth

Before smolting, average fish sizes corresponded directly with introduction time: early fish were consistently the largest and incubator fish were consistently smallest (Fig. 4). Masses at each sample were significantly different (all *P* values < 0.0001) among introduction groups. On average, masses as a percentage of incubator mass (lightest group) ranged from 50% heavier (early) to 14% heavier (late), with the middle group intermediate (36% heavier). Smolt sizes did not differ among introduction groups ($F_{[3,23]} = 1.60$, $P = 0.22$).

The fish size relationship among introduction groups was markedly different for fish that eventually smolted compared with fish that did not smolt. Previous masses of fish that did not smolt followed the pattern of average masses among groups (Fig. 4), with overall significant differences among groups across samples ($P < 0.00001$) and all pairwise differences were significant ($P < 0.00001$, independent linear contrasts). Overall, masses of smolts from the four groups were also significantly different across samples ($P = 0.003$), but linear contrasts revealed that the previous masses of the middle, late, and incubator smolts were not different from each other and that the overall difference was driven by masses of fish from the early group ($P = 0.00062$, linear contrast between early and other groups).

Growth rates, based on individuals caught on consecutive samples, varied significantly among introduction groups in two out of five intervals (Fig. 4). For all intervals, the ANCOVA interaction term between initial size and group was insignificant, allowing direct comparison among groups. As an illustration of growth differences, there were no differences among groups for the age-0+ fall to age-0+ winter interval, but there were significant growth differences among groups for the age-1+ postsmolt to age-1+ fall interval (Fig. 5). For this interval, the adjusted final size of the late group was 7% higher than the average of the other three groups. This is reflected in the higher regression line for this group in Fig. 5 and can also be seen in the steeper slope of

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Table 5. Model comparisons evaluating introduction group (G, first location in parentheses) and time (t, second location in parentheses) effects on apparent survival (ϕ) and probability of capture (p).

Model description	AIC_c	ΔAIC_c	AIC_c weights	No. of parameters	Deviance
$\phi(G, *)$, $p(*, t)$	2929.72	0.00	0.7871	10	306.01
$\phi(*, t)$, $p(*, t)$	2933.44	3.72	0.1222	12	305.67
$\phi(*, *)$, $p(*, t)$	2934.07	4.35	0.0893	7	316.43
$\phi(G, t)$, $p(*, t)$	2944.37	14.65	0.0005	30	279.54
$\phi(*, *)$, $p(G, t)$	2945.30	15.58	0.0003	23	294.99
$\phi(*, t)$, $p(G, t)$	2945.58	15.86	0.0003	30	280.74
$\phi(G, *)$, $p(G, t)$	2945.71	15.99	0.0003	26	289.19

Note: An asterisk (*) indicates a model with no group or time effect depending on location in parentheses. All possible model combinations were tested (19 models, see Materials and methods), but only models with AIC_c weights > 0 are shown in the table.

Table 6. Model comparisons evaluating variation in apparent survival (ϕ) among introduction groups (E, early; M, middle; L, late; I, introduction) with no time effect ($\phi(G, *)$).

Model description	AIC_c	ΔAIC_c	AIC_c weights	No. of parameters	Deviance
ϕ(E = M, L = I)	2926.32	0.00	0.59	8	306.66
ϕ(M, I = E = L)	2929.22	2.90	0.14	8	309.56
ϕ(E, M, L, I)	2929.72	3.40	0.11	10	306.01
ϕ(I, E = M = L)	2929.74	3.41	0.11	8	310.07
ϕ(E = I, M = L)	2933.07	6.75	0.02	8	313.41
ϕ(L, E = M = I)	2934.06	7.74	0.01	8	314.40
ϕ(E = M = L = I)	2934.07	7.75	0.01	7	316.43
ϕ(E = L, M = I)	2935.5	9.18	0.01	8	315.84
ϕ(E, M = L = I)	2935.98	9.66	0.00	8	316.32

Note: Capture probabilities for all models were modeled as time variant but without group differences ($p(*, t)$). The survival models with (ϕ(E, M, L, I)) and without group effects (ϕ(E = M = L = I)) from Table 5 are included for comparison.

Fig. 3. Abundances (±95% confidence interval, CI) of fish from the four introduction groups (early, ○; middle, □; late, ◇; incubator, △) estimated with a Jolly–Seber mark–recapture model. Abundances were scaled to the number of fish introduced into the stream for each group.

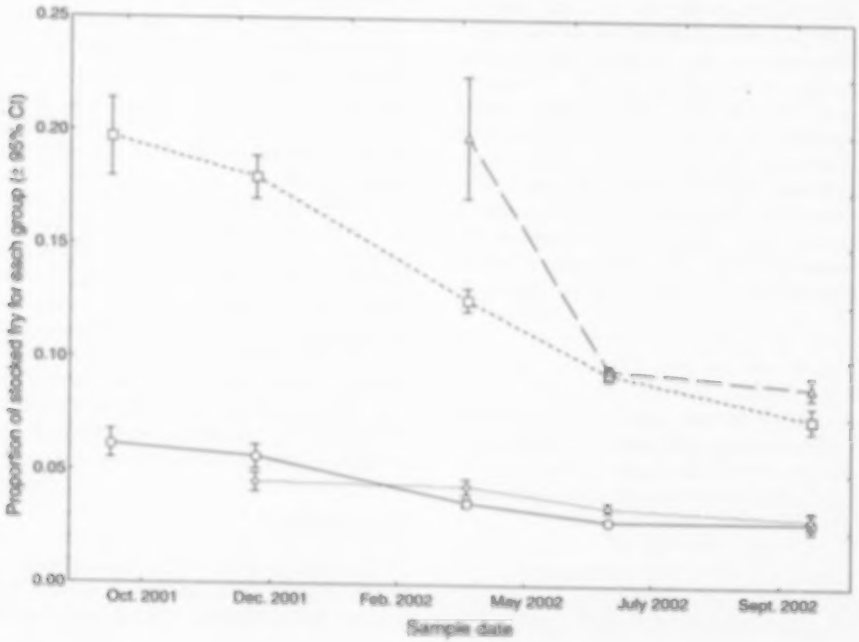

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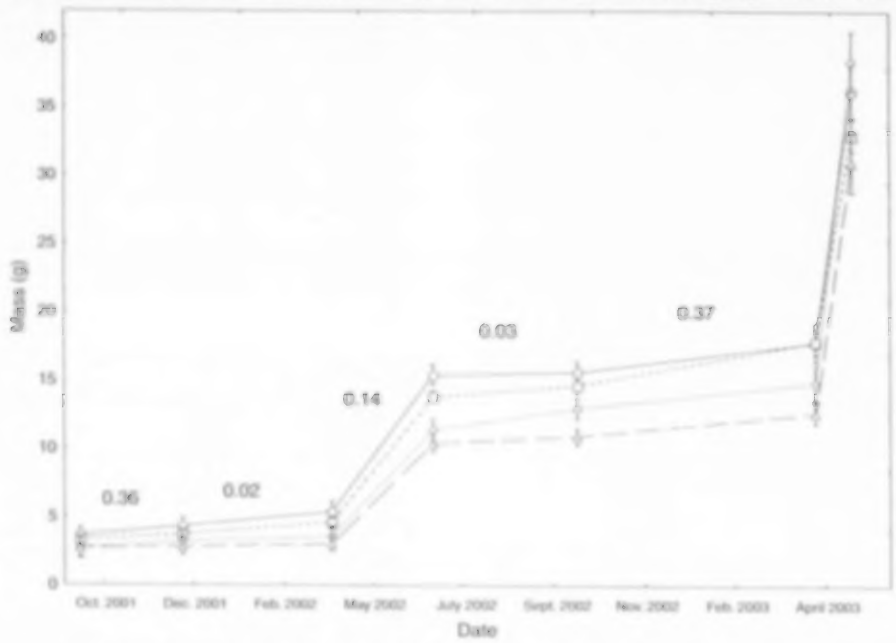
Fig. 4. Average (±95% confidence interval) masses of Atlantic salmon (*Salmo salar*) from the four introduction groups (early, ○; middle, □; late, ◇; incubator, △). Numbers are *P* values evaluating growth rate among introduction groups between consecutive samples.



line between average masses for age-1+ postsmolt to age-1+ fall interval (Fig. 4).

Laboratory study

Size trajectories were markedly different for early and late fish when they were grown alone or in mixed tanks ($P << 0.001$, tank effect $P = 0.88$ (treatment nested in tank)). When grown alone, late fish caught up in mass and even surpassed masses of early fish by October (Fig. 6), at which time the post-hoc test indicated that masses were not different ($P = 0.77$). In contrast, masses of late fish in the mixed treatment tanks were significantly suppressed compared with masses of late fish grown alone ($P << 0.001$). Not only were masses of late fish suppressed in the mixed tanks, but masses of early fish were significantly enhanced in the mixed treatment tanks compared with sizes of early fish grown alone ($P << 0.001$). By October, early/mixed fish were almost twofold heavier than late/mixed fish (Fig. 6). These results indicate that interaction between early and late fish can result in significant size divergence between stock times.

Life history

Parr maturity

Parr maturity (percentage of fish expressing milt) for the age-1+ fall sample varied among introduction groups (early, 51%; middle, 46%; late, 47%; incubation, 40%), but frequencies were not significantly different (Pearson $\chi^2 = 0.98$, df = 3, $P = 0.81$) from expected frequencies.

Smolt age

Overall, 69 smolts from the 2001 stocking year were captured in the smolt trap or read on the smolt antenna (Table 3). Of these, 21 were untagged, leaving 48 tagged fish (most untagged fish came from outside the study site). Twenty-nine of the tagged fish were caught in both the smolt trap and read on the antenna, 10 were read on the antenna only and nine were caught in the smolt trap only. The 10 fish that were read on the antenna only probably passed through a hole that was discovered in the smolt trap fence (open for 2 days maximum), and the nine fish that were not read on the antenna may have passed through the antenna at the same time as other tagged fish or were not read for other reasons. Overall, 40 fish belonged to one of the introduction groups: 33 were tagged and seven were untagged (left study site before possibility of tagging). The majority of smolts (43%, 17) were from the middle introduction group with fewer smolts from the early (11), late (7), and incubator (5) groups (Table 3).

In contrast to the smolt trap, the largest number of fish was from the incubator group in the sample following the smolt trap (age-2+ postsmolt; Table 3). The proportion of fish from the smolt trap sample and the sample following the smolt trap that were captured in the smolt trap (number in smolt trap/(number in smolt trap + number in postsmolt)) varied consistently with timing of introduction (early = 0.65; middle = 0.49; late = 0.37; incubator = 0.15). This observation demonstrates a clear life-history consequence resulting from variation in timing and manner (stocked vs. stream-reared) of stream introduction.

Discussion

The results of this study indicate that variation in the time (on the scale of weeks) and manner (stocked vs. stream-reared) of fry introduction can have substantial long-term ef-

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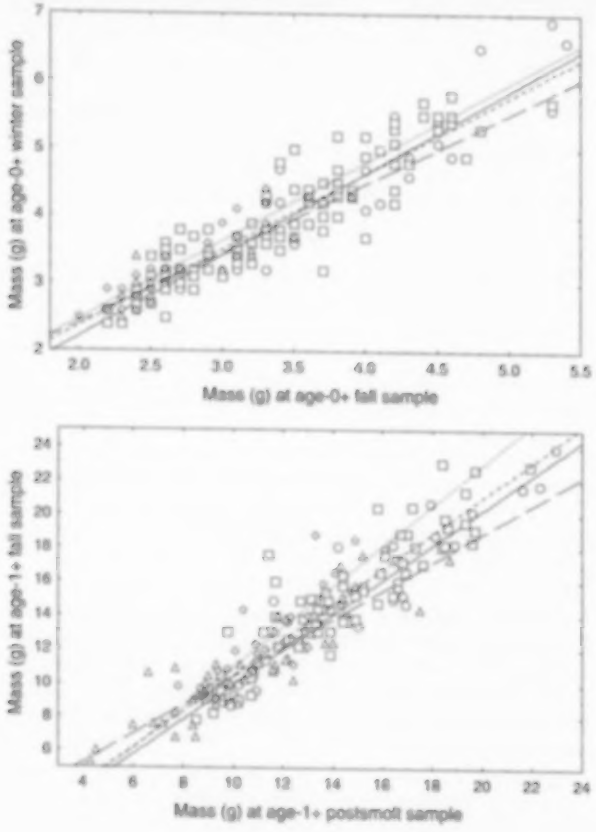
Fig. 5. Masses of individuals from the four introduction groups (early, ○; middle, □; late, ◇; incubator, △) caught on consecutive samples for two example intervals.



fects on parr size and survival and on expression of life histories. Differences in abundance among introduction groups were substantial and extended through to the 2-year-old smolt stage. Size variation among groups was also large and consistent before smolting, but because only the largest fish from each group (except for the early group) smolted at age 2+, there was no difference in smolt size among groups. Thus, smolt numbers, but not necessarily smolt size, may reflect short-term variation in stream introduction date.

Although date of introduction impacted both size and survival of salmon in the stream, the relative importance of mechanisms responsible for differences among introduction groups was not the same for size and survival. Early fish maintained a size advantage over all other introduction groups through freshwater residence. Two lines of evidence suggest that this difference in size resulted from prior residence advantage. First, early fish achieved their size advantage in spite of stocking under environmental conditions (high flows, low temperatures) likely to be less favorable for growth than the lower flows and higher temperatures experienced by fish introduced later (Elliott and Hurley 1997; Nislow et al. 2000; Forseth et al. 2001). Second, laboratory results indicated that early-stocked fish both suppressed the growth of late-stocked fish and gained an additional size advantage in the presence of late fish. These results are consistent with a number of previous studies documenting prior residence size advantage in juvenile salmonids (e.g., Mason and Chapman 1965; Chandler and Bjornn 1988; O'Connor et al. 2000). If fitness is related to size, this long-term size advantage, mediated by prior residence during emergence, supports Einum and Fleming's (2000) observation of strong selection for early emergence in Atlantic salmon.

Previous studies on prior residence advantage have not included temporal variation in environmental conditions, which is a common characteristic of stream environments, particularly during spring emergence (Poff and Huryn 1998; Jensen and Johnsen 1999; Nislow et al. 2000). For stocked fish, we found a clear link between low survival and high discharge following introduction. Low survival following high discharge is common in salmonids (Elwood and Waters 1969; Letcher and Terrick 1998), with strongest effects during short intervals after emergence (Jensen and Johnsen 1999). In temperate regions, high discharge is more likely early in the range of potential emergence dates (Nislow et al. 2000), with occasional spates later (as we observed in our study year); therefore, early emergers are more likely to face the negative consequences of high spring discharge that can range from complete year-class failure (in extreme flows) to moderate decreases in favorable postemergent foraging habitat. These consequences of high flows may counter or moderate the strong selective advantage of early emergence observed by Einum and Fleming (2000). The combination of environmental variability during and shortly after emergence and negative effects of prior residence will shape selection on introduction date. With our study cohort, we observed stabilizing selection on introduction date with early mortality related to effects of high discharge and late mortality probably resulting from a combination of prior residence effects and moderate discharge.

Results of the laboratory growth study indicated that size-based interactions in tanks could promote size divergence between fish introduced early and late. When reared together, sizes of early and late fish diverged substantially from each other compared with when groups were reared alone. Sizes of early and late fish were eventually similar when groups were reared alone, but we found significantly smaller sizes for late fish and significantly larger sizes for early fish when the groups were mixed. In the mixed tanks, it appears that sizes of the late fish were suppressed by the early fish. In addition, the early fish in the mixed tanks gained a size advantage compared with early fish reared alone because the early fish in the mixed tanks were exposed to one-half as many early fish as early fish in the early-alone tanks. The very strong size differences that we observed between mixed early and late fish in the laboratory were reduced in the field probably because stream habitat heterogeneity and habitat selection reduced size-based interactions among fish. In years like our study year, when the numbers of early fish were apparently depleted by high flows, the early fish that remained may have gained an additional growth advantage because they competed with fewer early fish. Likewise, the late fish may have suffered less growth depression because there were fewer early fish. In years with different flow patterns resulting in different relative representation among introduction groups, a variety of growth

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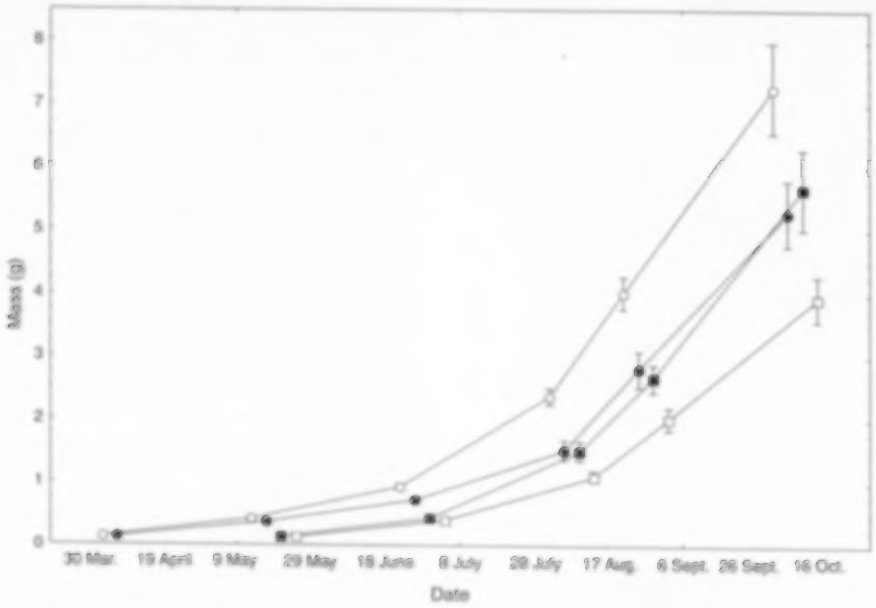
Fig. 6. Masses of early (circles) and late (squares) introduction group Atlantic salmon (*Salmo salar*) fry reared either separately (open symbols) or together (solid symbols) in laboratory tanks.



patterns among introduction times might be possible. For example, overall sizes could be depressed if lower early flows resulted in relatively more early fish. In this case, the greater number of early fish might depress both the average sizes of early fish (e.g., early alone treatment in laboratory study) and the sizes of late fish (e.g., late with early treatment in laboratory study).

In our analysis of survival, we examined survival differences among introduction groups in two ways that gave similar but not identical results. The first method (survival) was based on inferences from model selection procedures, was limited to the time period during which fish were tagged (age 0+ in the fall to age 2+ in the spring), and therefore did not include mortality prior to tagging. Our second approach (numerical) assessed overall survival from introduction to our last available abundance estimate and included losses from introduction to the last sample. Both approaches indicated that survival of the incubator fish was the highest. Differences in relative survival for the remaining groups suggested variation in the timing of survival between approaches. Based on the numerical estimate, survival of the middle group was similar to survival of the incubator group, which was much higher than both the early and late group survival estimates. However, middle group survival was not higher once the fish were large enough to tag (>60 mm), suggesting that the numerical advantage obtained by the middle fish occurred prior to tagging. In general, most of the mortality of juvenile salmonids occurs within the first few weeks after emergence. Based on the relatively high flows during introduction for the early and late fish, it appears that flow-related mortality soon after stocking may have reduced overall numbers of early- and late-stocked fish (but not incubator fish, see below). In a long-term study of a Norwegian River, Jensen and Johnsen (1999) found a strong negative relationship between survival and high discharge within 1 week of emergence. The relation between discharge and survival was weak for other life stages. In our study, post-introduction conditions (decreasing flows and increasing temperatures) were best for fish stocked during the middle period, which had the highest numerical abundance of all introduction groups.

Although it appears clear that abundances were strongly influenced by early variation in discharge and prior residence effects, it is less clear why survival estimates were different among groups once the fish were tagged. Inferences from mark–recapture model selection procedures indicated that survival of the incubator fish was highest, survival of early and middle fish was lowest, and survival of the late-stocked fish was intermediate. Because survival was highest for both groups of fish that were reared at the coldest temperatures (incubator and late) or in the stream (incubator only), there may be long-term effects of rearing environment and temperature on survival during the course of freshwater residence. Little is known about long-term effects of rearing environment on Atlantic salmon survival, but Nathanailides et al. (1995) demonstrated that rearing temperature can influence Atlantic salmon muscle fiber development and fish growth up to 3 weeks after first feeding. Extending the timeline further, Johnston et al. (2000) found persistent effects of rearing temperature on size and muscle fiber development to the smolt stage. In both cases, growth was faster for fish reared under native temperature regimes than under accelerated regimes. It is possible, then, that the lower survival for fish reared at warmer temperatures (early and middle groups) was due to persistent effects of rearing environment. It is also possible that the relatively high survival of the incubator fish was related to among- or within-day variance in temperature, which is higher in the stream than in the hatchery water, but we know of no reports examining long-term effects of variance in rearing temperature on survival. Con-

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trary to our findings, fish reared in native temperature regimes were always larger than fish reared in warmer temperatures (Nathanailides et al. 1995; Johnston et al. 2000), even though the warmer regimes produced earlier hatch dates. In our study stream, the fish reared in the stream were consistently the smallest fish, reinforcing the suggestion that the smaller size of the incubator fish resulted from prior residence growth depression.

Many researchers have found a strong relationship between previous size and later expression of life histories in juvenile Atlantic salmon (Metcalfe 1998; Thorpe et al. 1998; Letcher and Gries 2003). Fish that will smolt the following spring are usually much larger in the preceding autumn than fish that will delay smolting for a year (Thorpe 1977; Heggenes and Metcalfe 1991), and males that will mature as parr in the autumn are typically larger or growing faster in the spring than males that will not mature (Dalley et al. 1983; Berglund 1992; Simpson 1992). If life-history transitions were based solely on size differences, we might expect wide variation in expression of life histories among the introduction groups. In contrast, we found that the extent of parr maturation was not significantly different among introduction groups despite substantial group variation in size. The first explanation for the lack of correspondence between size and maturity is that all fish were large enough or growing fast enough to exceed the maturation threshold. The second explanation is that maturation is more a function of growth variation during particular time intervals than of size variation. Despite size differences, growth rates among groups were similar during the time of year that mass differences are first expressed between mature and immature fish (Letcher and Gries 2003). Our parr maturation result generally supports the model of Thorpe et al. (1998), who proposed that parr maturation depends on current and future expected growth over critical intervals. In addition, Thorpe et al. (1998) proposed that smolt age also depended on current size and expected growth, such that larger, faster-growing fish will smolt at a younger age. We found that fish smolting at age 2+ were the largest fish of any group and that average sizes of smolts from the different groups (except early fish, which were larger) were not different from each other. The comparatively large size and lack of difference in size of age-2+ smolts among groups suggests a common size threshold for early smolting among introduction groups. It also suggests that an early disadvantage (stocked/emerged late) does not necessarily negate the opportunity to smolt early; some fish were able to compensate for an early size disadvantage.

In a direct comparison of hatchery-reared (late group) and stream-reared (incubator group) fish, we found that survival of the stream-reared group was much higher than survival of the hatchery-reared group. Both groups were introduced into the stream at similar developmental stages, at approximately the same date and time of day, and were maternal half sibs. Besides the possibility of persistent rearing temperature effects on survival, the reason for the higher incubator group survival is unknown. Differences in aggression, energy expenditure and feeding, predator avoidance, and dispersal between hatchery and wild fish (see recent review by Weber and Fausch (2003)) could all contribute to the survival difference between stocked and incubator fish. The higher incubator group survival introduces several important considerations for management of stocking efforts. First, the higher survival of stream-reared fish suggests that better introduction success could be achieved by incubating fish in the stream rather than stocking them after hatchery rearing. Stream rearing large numbers of eggs in large introduction programs like that in the Connecticut River presents logistical difficulties (>10^7 eggs over 29 000 km^2) but may be possible for smaller programs or for eggs of special concern. Second, the emergence date of our stream-reared fry was near the end of the typical range of stocking dates in the Connecticut River. In natural populations, selection on emergence date has shaped the emergence date to maximize long-term fitness (Einum and Fleming 2000), so it is possible that the mismatch of current Connecticut River stocking dates to stream-reared emergence dates could result in suboptimal fry survival. In addition to survival, it is also important to consider size effects and possible life-history consequences of stocking strategy. In our study stream, the smaller size of the incubator fish did not result in significantly lower percentages of maturing male parr. Some early group fish did compensate for early size disadvantage and smolted at age 2+, although the ratio of incubator smolts to incubator fish that delayed smolting was substantially depressed compared with that of fish from the early and middle groups. In streams with slower growth, there could be further shifts in proportions of fish expressing life histories at certain ages that result from variation in timing of introduction. A thorough cost–benefit analysis that includes variation in growth, survival, and life-history expression resulting from effects of both manner and timing of fry introduction to evaluate the relative effectiveness of large-scale stocking vs. large-scale stream rearing of embryos in a large restoration effort like that of the Connecticut River would be useful. Overall, results of our field study suggest that mode and timing of introduction interacting with environmental variation and effects of prior residence can have substantial impact on growth, survival, and life-history expression of stream-dwelling Atlantic salmon.

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The costs of habitat utilization of wild, farmed, and domesticated juvenile Atlantic salmon (*Salmo salar*)[1]

Eva C. Enders, Daniel Boisclair, and André G. Roy

Abstract: We compared morphometry and total swimming costs of wild, farmed (first-generation hatchery progeny of wild progenitors) and domesticated (seventh-generation progeny of the Norwegian aquaculture strain) juvenile Atlantic salmon (*Salmo salar*). Respirometry experiments were performed to assess total swimming costs of fish ranging in size from 4.0 to 16.1 g wet mass at a water temperature of 15 °C. Fish were subjected to flow conditions of low and high turbulence. Total swimming costs increased significantly with intensity of turbulence and were, on average, 1.4 times higher at high than at low turbulence. Total swimming costs were 2.4- to 4.0-fold higher than predicted by forced swimming models developed under conditions that minimize flow heterogeneity. Total swimming costs of wild and farmed fish were not statistically different (average difference = 6.7%). Hence, swimming costs models developed using farmed fish may be used to estimate swimming costs of wild fish. However, domesticated fish had total swimming costs 12.0% to 29.2% higher than farmed or wild fish. This may be related to domesticated fish having deeper bodies and smaller fins.

Résumé : Nous avons comparé la morphométrie et les coûts énergétiques totaux de nage des juvéniles du saumon atlantique (*Salmo salar*) sauvages, piscicoles (première génération en pisciculture issue de géniteurs sauvages) et domestiques (septième génération en pisciculture issue de la souche d'aquaculture norvégienne). Les expériences respirométriques ont été réalisé afin d'estimer les coûts énergétiques totaux de poissons de 4,0 à 16,1 g à une température de 15 °C. Les poissons étaient soumis à une faible et une forte condition turbulente de l'écoulement. Les coûts énergétiques totaux de nage augmentaient significativement avec l'intensité turbulente; ils étaient en moyenne 1,4 fois plus élevés à forte turbulence qu'à faible turbulence. Les coûts énergétiques totaux de nage étaient de 2,4 à 4,0 fois plus élevés que ceux prédits par les modèles de nage forcée. Les coûts énergétiques totaux des poissons sauvages et piscicoles n'étaient pas significativement différents (différence moyenne = 6,7 %). Ainsi, les modèles de coûts énergétiques de nage développés avec les poissons piscicoles peuvent être utilisés afin d'estimer les coûts énergétiques des poissons sauvages. Cependant, les poissons domestiques avaient des coûts énergétiques totaux de 12.0 % à 29.2 % plus élevés que les poissons piscicoles ou sauvages. Ceci pourrait être relié au fait que les poissons domestiques avaient un corps plus haut et des nageoires plus petites.

Introduction

Swimming costs of stream-dwelling fish are generally estimated using forced swimming models (Hughes and Dill 1990; Sabo et al. 1996; Guensch et al. 2001). These models are derived from experiments conducted with fish swimming at a steady speed in a flume respirometer designed to minimize flow heterogeneity (Brett 1964; Beamish 1978). However, in their natural environment, stream-dwelling fish are confronted by highly turbulent flow. In these environments, turbulence is associated with a wide range of instantaneous velocities to which fish have to continuously adjust their swimming speed and their body position to maintain their location in the surrounding flow field. It has been demonstrated recently that turbulence affects the behavior and swimming performance of stream-dwelling fish. Pavlov et al. (2000) observed a decrease in sustained and critical swimming speeds with an increase of turbulence intensity for two lowland fish species (*Gobio gobio* and *Rutilus rutilus*), indicating that the energy expenditures are higher in

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E.C. Enders[2,3] **and D. Boisclair.** Université de Montréal, Département de sciences biologiques, C.P. 6128, Succursale Centre-ville, Montréal, QC H3C 3J7, Canada.
A.G. Roy. Université de Montréal, Département de géographie, C.P. 6128, Succursale Centre-ville, Montréal, QC H3C 3J7, Canada.

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[2]Corresponding author (e-mail: enderse@dfo-mpo.gc.ca).
[3]Present address: Fisheries and Oceans Canada, Ecological Sciences Section, P.O. Box 5667, St. John's, NL A1C 5X1, Canada.

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Table 1. Number of respirometry experiments per flow condition for four groups of juvenile Atlantic salmon ((1) wild fish, (2) farmed fish from the Sainte-Marguerite River, (3) farmed fish from the Imsa River, and (4) domesticated fish), range of body mass, and total swimming costs under low and high turbulence intensities with the same mean flow velocity of 23 $cm \cdot s^{-1}$ and two different standard deviations of 5 $cm \cdot s^{-1}$ and 8 $cm \cdot s^{-1}$.

	Group 1	Group 2	Group 3	Group 4
Experiments per flow condition	8	8	5	6
Body mass (g)	4.15–13.02	4.90–16.01	3.95–16.11	7.73–14.06
Total swimming costs (mg $O_2 \cdot h^{-1}$)				
Low turbulence intensity	2.10–4.40	2.68–6.00	2.11–6.59	3.99–6.25
High turbulence intensity	2.83–7.21	3.74–8.00	2.67–8.02	5.24–8.29

turbulent flow. In a preliminary study, we demonstrated that net swimming costs (total respiration rate of unfed fish minus the standard metabolism) of juvenile Atlantic salmon (*Salmo salar*; JAS) under fluctuating flow velocities may be two- to four-fold higher than those predicted by forced swimming models (Enders et al. 2003). For practical reasons, the respirometry experiments were performed with fish of hatchery origin. However, Fleming et al. (1994) demonstrated that cultured JAS diverged significantly from their principal wild founder population in body morphology, having smaller heads and fins and narrower caudal peduncles. The morphological differences that exist between wild and cultured fish may also affect swimming performance and, therefore, the applicability of swimming costs models developed using cultured fish to wild populations. This may, in turn, affect estimates of the net energy gain and the habitat quality values generated by bioenergetics models (Ney 1993).

The objectives of our study were (*i*) to compare morphometric variables among wild JAS, farmed JAS (first-generation hatchery progeny from wild progenitors), and domesticated JAS (seventh-generation progeny of a Norwegian aquaculture strain), (*ii*) to confirm the effect of flow turbulence on the energetic cost of swimming, and (*iii*) to quantify the differences that may exist in the total swimming costs (cost of swimming + standard metabolism) of the different groups of fish. This study was especially designed to assess the applicability of respirometry models developed with cultured JAS to wild JAS.

Materials and methods

We accomplished our objectives by taking photographs of 20 individuals from each of the four groups of fish that differed in geographical origin (Canada or Norway) and degree of domestication (wild, farmed, or domesticated). From these photographs, we measured 30 morphometric variables describing different features of the body dimensions. Respirometry experiments were performed during which we subjected individual fish to two different types of turbulent flow characterized by the same mean flow velocity but two different standard deviations of flow velocity. Experiments were therefore performed under two levels of turbulence intensity (standard deviation/mean flow velocity). Total swimming costs (cost of swimming + standard metabolism) obtained for the two turbulence intensities were compared for four fish groups. All fish were adapted to a water temperature of 15 °C for a period of 3 weeks before starting the respirometry experiments. The body mass of the fish used for our experiments ranged from 4.0 to16.1 g wet mass (Table 1).

Fish

We obtained juvenile Atlantic salmon (JAS) for our experiments from four different sources. (1) Wild JAS from the Sainte-Marguerite River (Saguenay Region, Québec, Canada, 48°15′N, 69°55′W) were collected with a backpack electrofisher (model 12-B; Smith-Root Inc., Vancouver, Washington, USA). Fish were transferred to the laboratory at the Université de Montréal and kept in a 500-L Living Stream aquarium (model LSW 700; Frigid Units Inc., Toledo, Ohio, USA). Flow in these tanks was approximately 5 $cm \cdot s^{-1}$. Wild fish did not accept commercial pellets and were fed daily with red mosquito larvae (San Francisco Bay Brand™, Newark, California, USA). (2) Farmed JAS from the crossing of wild progenitors that originated from the Sainte-Marguerite River were obtained from the Pisciculture de Tadoussac (operated by the Société de la Faune et des Parcs du Québec, Canada). The juveniles were transferred to the Université de Montréal and kept under conditions (tank and flow velocities) identical to those of wild fish. However, farmed fish from the Pisciculture de Tadoussac were fed daily with commercial food pellets (Corey Feed Mills Ltd., Fredericton, New Brunswick, Canada). (3) Farmed JAS from the crossing of wild progenitors that originated from the Imsa River were provided by the Norwegian Institute of Nature Research (NINA) Research Station at Ims (Rogaland, Norway, 58°59′N, 5°58′E). The fish were kept in 1-m^2 tangential flow tanks supplied with flow-through freshwater from the Imsa River. The flow velocity in the tanks was approximately 5 $cm \cdot s^{-1}$. These fish were fed commercial food pellets (EWOS®, Bergen, Norway) using automatic feeders. (4) Domesticated JAS that originated from the Norwegian National Breeding Program at Sunndalsøra (Aquagen, Norway) were taken as eyed eggs to the NINA Research Station. The Sunndalsøra salmon were developed for the Norwegian fish farm industry and have been bred selectively since 1971 to attain certain characteristics such as increased growth, delayed maturity, and disease resistance. The first-generation fish were derived from 40 different wild salmon populations. However, after four generations, the stock was dominated by individuals coming from only one to three populations characterized by fast-growing and late-maturing fish. The fish that we studied were seventh generation of the first brood line (Gjedrem et al. 1991). The domesticated JAS were kept

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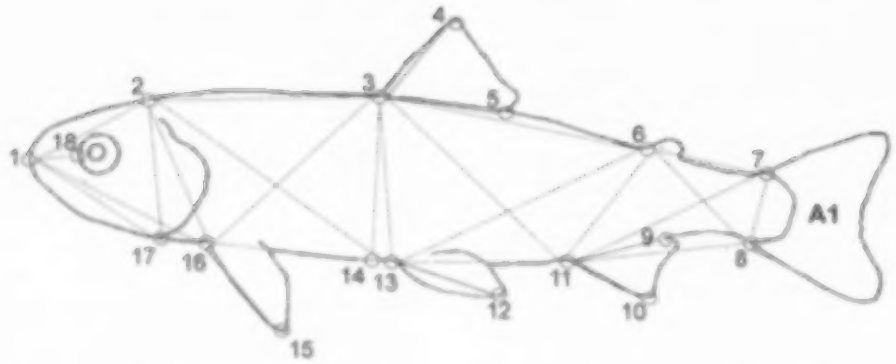
Fig. 1. Location of 18 landmarks (open circles), 23 trusses (dotted lines), six fin lengths (solid lines), and the caudal fin area (A1): (1) anterior tip of snout at upper jaw; (2) most posterior aspect of neurocranium; (3) origin of dorsal fin; (4) distal tip of dorsal fin; (5) insertion of dorsal fin; (6) origin of adipose fin; (7) anterior attachment of dorsal fin membrane from caudal fin; (8) anterior attachment of the ventral membrane from caudal fin; (9) insertion of anal fin; (10) distal tip of anal fin; (11) origin of anal fin; (12) distal tip of pelvic fin; (13) origin of pelvic fin; (14) point of the ventral surface of the body directly below the anterior dorsal fin origin; (15) distal tip of pectoral fin; (16) origin of pectoral fin; (17) posterior-most point of the maxilla; and (18) anterior-most edge of the orbit.



under conditions (tank, flow velocities, food, feeding regime) identical to those of farmed fish of the Imsa River.

Morphometric measurements

Individual fish from each group (n = 20) were anaesthetized (clove oil; 0.6 mg·L^{-1}) and placed left side up on a moist, blue carpet that had two rulers with millimetre scales along the lower and left edges. Anal, dorsal, and caudal fins were erected and small pieces of white paper were placed under the pectoral and pelvic fins to increase their visibility. Images were taken using a tripod and a video camera (ES610 fitted with a 50-mm lens; Canon Canada Inc., Mississauga, Ontario) set at a fixed distance of 40 cm from the fish. The images were analyzed using the image analysis software SigmaScan Pro 5.0 (Statistical Solutions, Saugus, Massachusetts, USA). Spatial coordinates of 18 morphometric landmarks as described in Winans (1984) and Swain et al. (1991) were taken (Fig. 1).

The 18 morphometric landmarks were used to calculate 23 interconnected distance variables defining different aspects of the dimensions of a fish (subsequently referred to as truss measurement; Fig. 1). The truss network is a series of measurements calculated between the landmarks that form a regular pattern of contiguous quadrilaterals or cells across the body. Compared with more conventional sets of measurements, the truss network has the advantage of providing an equal coverage of the entire body (Strauss and Bookstein 1982). In addition to the truss network, six fin measurements were calculated from the landmark coordinates, and the caudal fin area was measured. Consequently, we obtained 30 morphometric variables describing different aspects of body dimensions. To measure the precision of the digitizing approach, 10 individuals were measured five times. The standard deviation over the five replicates of every morphometric variable was estimated for each of the 10 fish. The average standard deviation over 10 fish was used as an estimate of measurement error. The measurement error was always less than 0.5 mm.

Principal components analysis was then used to describe the body shape independent of body size (Jolicoeur 1963). Therefore, all morphometric variables were log-transformed. This procedure allows body size, for which we are trying to control during our comparative analyses, to become an additive component of every variable. The first principal component of the log-transformed data was expected to represent a combination of the morphometric variables correlated to the general body size and was therefore removed from the data set. The dorsal fin height was the only morphometric variable that did not vary with body size. However, such variables dominate the subsequent shape components and artificially influence the importance of these variables. Therefore the dorsal fin height was omitted from the principal components analysis as suggested by Somers (1986). The loadings of the 29 remaining size-corrected morphometric variables from the second and third principal components were used to compare the four fish groups. The significance of the morphological differences between the four groups was assessed using multivariate analysis of variance (MANOVA) followed by Scheffé's post hoc test.

Respirometry

The respirometry system consisted of a transparent Plexiglas® container (24 L; 60 cm × 20 cm × 20 cm) with a lid that could be hermetically sealed. The respirometer was placed in a water bath to maintain water temperature of 15 °C during the experiments. The details of the experimental design are described in Enders et al. (2003) and are presented here only in a summarized version. The respirometer contained two pumps and a bottle-shaped swimming chamber. The shape of the swimming chamber was selected to ensure that fish could not avoid the water flow during the experiments. The narrow neck of the swimming chamber was connected to pump 1 (model 1750; Jacobs Canada Inc., Mississauga, Ontario), which generated the turbulent flow in the swimming chamber by recirculating water within the respirometer. The swimming chamber contained two grids.

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The grids consisted of nylon mesh 9 cm in diameter perforated with 2 mm × 2 mm holes. The grids were located in the "upstream" and "downstream" sections of the swimming chamber. The upstream grid was used to produce a spatially uniform fine turbulence flow structure within the swimming chamber (Tritton 1988). Spatially uniform fine turbulence corresponds to small-scale turbulence without persistent eddies. The downstream grid was designed to force the fish to remain in the swimming chamber without interfering with the flow. Pump 2 (model 402; Powerhead, Montréal, Québec) served two purposes. Before an experiment, pump 2 was used to create water exchange between the respirometer and the aquarium, hence providing oxygenated water to the respirometer. During an experiment, pump 2 was used to transfer water from the respirometer to the oxygen meter. Fish swimming costs were quantified by measuring the oxygen depletion over time with an oxygen meter (InTap 565; Mettler Toledo, Mississauga, Ontario; ±0.01 mg $O_2 \cdot L^{-1}$).

Characteristics of flow structures

Turbulence in the swimming chamber was created by modulating the electric current that powered pump 1. Four components of the electric current were adjustable: (1) the maximal electric current, which determines the maximal flow velocity, (2) the minimal electric current, which determines the minimal flow velocity, (3) the frequency at which the current was reduced, which introduced pulsations into the water flow, and (4) the duration of the reduced current. Flow velocities were measured using an Acoustic Doppler Velocimeter (ADV; Sontek, San Diego, California, USA). The ADV allowed us to record the three orthogonal velocity components of the flow (streamwise, U; vertical, V; lateral, W) at a frequency of 25 Hz. The volume sampled by the ADV (0.25 cm^3) is located 5 cm away from its probe so that the perturbation of the measured flow by the probe is minimized. Turbulence, quantified at the beginning of the suite of experiments in Canada and in Norway, was aimed at testing the effect of flow conditions on total swimming costs. Turbulence was quantified in the absence of fish to avoid interference caused by fish on the recordings. The presence of fish would not have changed the turbulence faced by the fish. However, if a fish had stayed in the swimming chamber, it would have interfered with the velocity measurements because the ADV measurements are based on the acoustic Doppler effect and the assumption that the particles in the flow have the same velocity as the flow. The fish, however, is actively swimming in chamber, having a ground speed of approximately zero. For every flow condition, a velocity time series was recorded for a period of 5 min. The ADV permitted us to define the settings of the components of the electric current that could create two different flow conditions determined by one mean streamwise flow velocitiy, $\bar{u}$ (23 $cm \cdot s^{-1}$) and two different standard deviations of the streamwise flow velocity, u_{SD} (low turbulence condition = 5 $cm \cdot s^{-1}$; high turbulence condition = 8 $cm \cdot s^{-1}$). Flow turbulence intensities (standard deviation/mean flow velocity) for each condition were 0.22 and 0.35, respectively. The means and the standard deviations were estimated from the 5-min velocity time series sampled at a frequency of 25 Hz. The two experimental flow conditions were selected for our experiments because they are within the range of mean flow velocities (5–40 $cm \cdot s^{-1}$; DeGraaf and Bain 1986; Guay et al. 2000) and the range of standard deviations of flow velocity (4–14 $cm \cdot s^{-1}$) at the focal point of the JAS in nature (Enders et al. 2005). In this article, we use the term high turbulence to facilitate the presentation of our results and not to insinuate that the high turbulence represents a condition close to the maximum turbulence experienced by fish in the field.

Stability and repeatability tests with three velocity time series recorded at the beginning and end of a suite of experiments were conducted in a previous study. These tests demonstrated that our apparatus generates consistent and reproducible turbulent flow structures (Enders et al. 2003). The repeatability of each of the two experimental flow structures created by our apparatus was again tested using a one-way analysis of variance (ANOVA). This ANOVA was performed to compare the mean streamwise flow velocities during the time series recorded before a suite of experimental observations. The repeatability of the standard deviations of the flow velocities was tested using the same approach with Levene's test of the homogeneity of variance (SPSS Inc., Chicago, Illinois, USA).

Total swimming costs

We used a single fish selected at random from our stock of experimental fish for each experiment. The fish was not fed for 2 days before the experiment to avoid increased metabolic rates associated with digestion (Brett and Groves 1979). Twenty-four hours before the beginning of an experiment, the fish was introduced into the swimming chamber to allow it to adapt to the experimental conditions. After the introduction of the fish into the swimming chamber, the respirometer was sealed without residual air bubbles. No observation was made below 7.6 mg $O_2 \cdot L^{-1}$ to minimize the influence of low oxygen concentration on fish behavior (Beamish 1978).

We monitored fish behavior during each experiment to ensure that fish were continuously swimming. An image of the position held by the fish within the swimming chamber was automatically registered every 10 min with a web cam (Sony Electronics Inc., Oradell, New Jersey, USA). In addition, during the last 30 min of the experiment, the fish was continuously filmed by a video camera (WV-BL602; Panasonic Canada Inc., Lachine, Québec). Hence, we assume that if a fish is always in a swimming position during a series of images registered at 10-min intervals and if a fish swims continuously during the last 30 min of an experiment, then it was swimming continuously against the flow structures created by our apparatus. An experiment ended after 6 h, at which time the fish was removed from the respirometer, anaesthetized (clove oil; 0.6 mg·L^{-1}), weighed (g wet mass), and measured (total length, cm). The biological oxygen demand (BOD) was determined within 6 h of an experiment using the same procedure but without fish.

The total oxygen consumption rate of the fish (Vo_2; mg $O_2 \cdot h^{-1}$) was estimated as

$$(1) \qquad Vo_2 = \Delta O_2 / \Delta t \cdot V_w - BOD$$

where ΔO_2 is the difference in oxygen concentration between two successive measurements (mg $O_2 \cdot L^{-1}$), Δt is the

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time interval of 0.5 h between two consecutive measurements, V_w (22.6 L) is the volume of water in the closed respirometer, and BOD is the biological oxygen demand by microorganisms in the water (mg $O_2 \cdot h^{-1}$). Because we measured oxygen concentration within the swimming chamber at 30-min intervals over 6 h, we obtained 12 Vo_2 values per experiment. We then calculated the total swimming costs (C_R; cost of swimming + standard metabolism) as the mean of the Vo_2 values obtained for each experiment.

Before statistical analyses, total swimming costs and body masses were log-transformed, and the residuals were tested for normality using graphical probability plots and for homogeneity of variance using Levene's test. A two-way ANOVA was performed to determine the effect of the fish groups and the turbulence intensities on the total swimming costs. In these analyses, body mass was used as a covariate. Scheffé's post hoc test was used to verify which of the four fish groups were significantly different. The two-way ANOVAs were performed using SuperANOVA 1.11 statistical packages (Abacus Concepts Inc. 1991).

Results

Comparison of the morphometric variables for the four different fish groups

Principal components analysis indicated differences in body shape among the four groups of fish (Fig. 2*a*). The first principal component (PC1) summarized the strong correlations between the morphometric variables and the total body length ($r^2 = 0.88$, $p = 0.001$). The second and third principal components (PC2 and PC3) described the variation in body shape, statistically independent from total body length ($r^2 = 0.07$, $p = 0.15$ and $r^2 = 0.00$, $p = 0.86$, respectively). PC1 accounted for 76.3% of the total variance in the morphometric variables. PC2 explained 6.8% and PC3 accounted for 5.0% of the total variance in morphometric variables (Table 2). PC2 involved a contrast between body depth, caudal fin area, and measurements in the head region. Domesticated fish had positive scores on PC2, indicating a deep body shape with smaller caudal fins and smaller heads, whereas the wild fish and farmed fish from the Sainte-Marguerite River had negative scores on PC2, indicating slender bodies with greater caudal fins and larger heads. The body height of domesticated JAS was 7.9% to 8.6% larger than that of wild JAS. The caudal fin and the head of domesticated JAS were on average 16.7% and 26.7% smaller than those of wild JAS. In this respect, farmed fish from the Imsa River were intermediate between farmed fish from the Sainte-Marguerite River and domesticated fish. The four groups showed significant differences for the PC2 (MANOVA, $F_{[3,79]} = 135.2$, $p < 0.001$). PC3 was defined by tail length and dorsal and anal fin lengths. Farmed fish from the Sainte-Marguerite River scored positively on PC3, indicating shorter tail lengths and smaller dorsal and anal fin lengths, whereas the wild fish and farmed fish from the Imsa River tended to score negatively on PC3, indicating longer tail lengths and larger dorsal and anal fin lengths. The tail lengths of farmed JAS from the Sainte-Marguerite were 19.3% to 17.9% shorter than those of wild JAS. The dorsal and anal fin lengths of farmed JAS of the Sainte-Marguerite were on average 26.6% and 3.4% smaller than those of wild JAS. Domesticated fish did not score on PC3. Mean PC3 scores differed significantly between the four fish groups (MANOVA, $F_{[3,79]} = 31.2$, $p < 0.001$). Scheffé's post hoc test showed that PC3 scores of wild JAS differed significantly from those of farmed and domesticated JAS ($p < 0.01$). The PC3 scores of farmed fish were significantly different from those of domesticated JAS ($p < 0.01$). However, the PC3 scores of the two groups of farmed JAS from the Sainte-Marguerite River and the Imsa River were not significantly different ($p = 0.98$).

Characteristics of flow structures

The mean values of the streamwise flow velocities obtained for the two different turbulent conditions were consistent with the targeted value of 23 cm·s^{-1} (Table 3). The mean streamwise flow velocities ranged from 23.01 to 23.04 cm·s^{-1}. Standard deviations of the streamwise flow velocity ranged from 5.13 to 5.15 cm·s^{-1} under low turbulent conditions (target = 5 cm·s^{-1}). Corresponding values for the high turbulent conditions (target = 8 cm·s^{-1}) ranged from 7.99 to 8.07 cm·s^{-1}. The turbulence intensity was 0.22 for the low turbulence condition and 0.35 for the high turbulence condition. The mean vertical flow velocities ranged from –0.15 to 0.92 cm·s^{-1}, with the standard deviation of the vertical flow velocity ranging from 4.92 to 7.56 cm·s^{-1}. The mean lateral flow velocities were close to zero, ranging from 0.09 to 0.33 cm·s^{-1} with standard deviations between 5.41 and 7.69 cm·s^{-1}.

The time series of the streamwise flow velocity for the two flow conditions clearly indicated that the flow created by our apparatus was turbulent with a range of velocity fluctuations (Fig. 3). For the two turbulence conditions, $\bar{u}$ did not vary significantly among the recordings performed for the four velocity time series (variation = 0.1%, ANOVA, $F_{[3,30003]} = 0.05$, $p = 0.98$). Similarly, for any given flow condition, u_{SD} obtained for the two velocity time series did not vary significantly (variation = 0.4%, Levene's statistic$_{1,15000} = 2.50$, $p = 0.12$, and variation = 1.0%, Levene's statistic$_{1,15000} = 0.55$, $p = 0.81$, respectively). These results confirmed our previous findings that the turbulent flow structures created by our apparatus were repeatable and stable (Enders et al. 2003).

Total swimming costs

Total swimming costs varied fourfold among treatments depending on fish body mass (Fig. 4). The predicted total swimming costs for a 10-g wild JAS at low turbulence intensity (3.80 mg $O_2 \cdot h^{-1}$) was 45.9% lower than the predicted value for high turbulence intensity (5.55 mg $O_2 \cdot h^{-1}$; Table 4). Total swimming costs differed among the four groups of fish (ANOVA, $F_{[3,38]} = 7.20$, $p = 0.0006$) and increased with turbulence intensity ($F_{[1,38]} = 0.01$, $p = 0.0001$) and body mass ($F_{[1,38]} = 0.03$, $p = 0.0001$). The interaction terms between fish group, turbulence intensity, and body mass were not significant ($0.66 < p < 0.95$) and indicated that the direction of the effect of turbulence intensity and body mass on total swimming costs was similar among fish groups. Total swimming costs of wild fish were not significantly different from those of farmed fish (difference ranging from 2.3%

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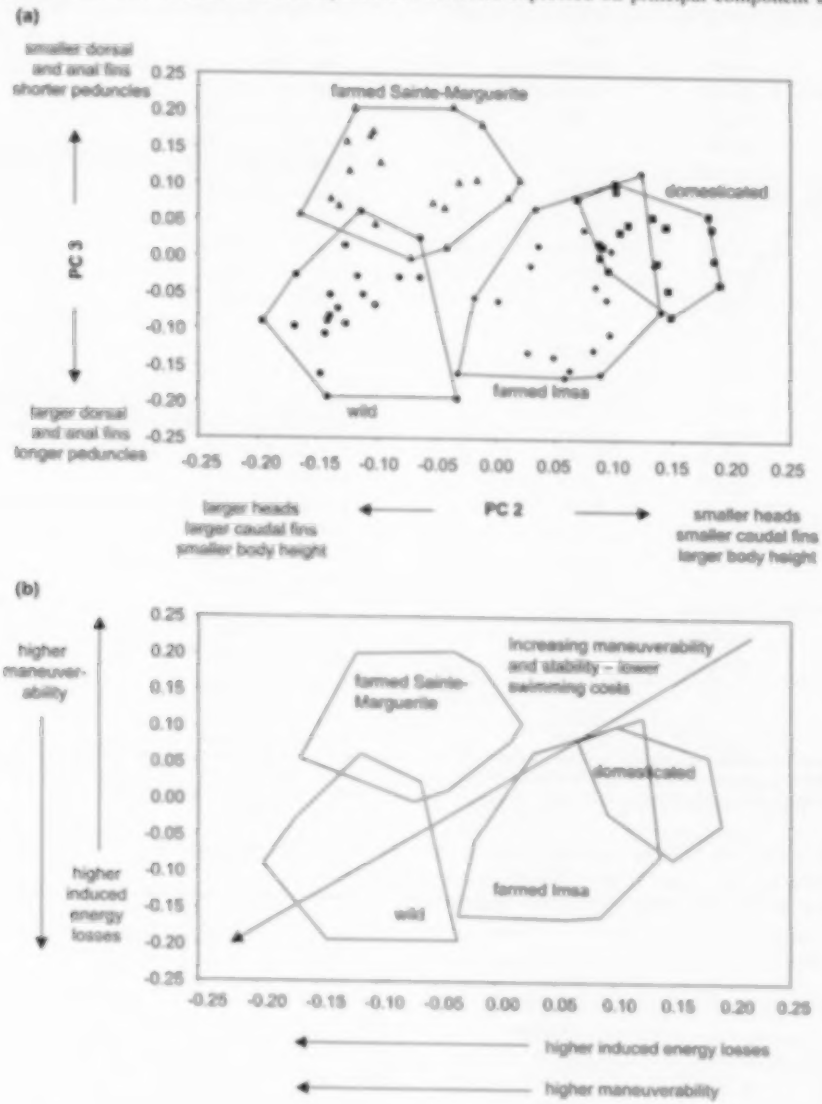
Fig. 2. (*a*) Principal components analysis of the morphometric variables of wild fish (●), farmed fish from the Sainte-Marguerite River (▲), farmed fish from the Imsa River (◆), and domesticated fish (■). Morphometric variables, which have loadings on principal component axes 2 and 3, are noted, and arrows indicate the direction of the correlation. (*b*) Arrows indicate the direction of maneuverability, and induced energy losses increase because of the morphometric variables expressed on principal component axes 2 and 3.



to 11.2%, $p = 0.08$). Similarly, the total swimming costs of the two groups of farmed fish (Sainte-Marguerite River and Imsa River) were not significantly different ($p = 0.73$). However, the total swimming costs for wild fish vs. domesticated fish differed significantly ($p = 0.0001$). Total swimming costs predicted for a 10-g wild fish were 29.2% lower under low turbulence intensity and 15.2% lower under high turbulence intensity than the total swimming costs for domesticated fish (Fig. 5). Total swimming costs predicted for a 10-g farmed fish were also significantly different from those for domesticated fish ($p = 0.01$). The total swimming costs for a 10-g farmed fish were 12.5% (high turbulence intensity) to 16.2% (low turbulence intensity) lower than those for a domesticated fish of the same mass.

Discussion

The morphology of the domesticated JAS has been shown to be different from that of the wild fish, with the head being smaller, the body more robust, and rayed fins smaller (Fleming and Einum 1997). In contrast, wild fish have a more slender body shape and larger fins than domesticated JAS. Our work supports these findings by showing that domesticated fish have deeper bodies and smaller caudal fins and

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Table 2. Loadings of the morphometric variables along the first, second, and third principal component axes (PC1, PC2, and PC3, respectively).

Variable	PC1	PC2	PC3	Description
1–2	–0.137	**–0.217**	0.036	**Forehead length**
2–17	–0.176	0.013	0.023	Head depth 1
2–16	–0.175	0.020	0.096	Head depth 2
2–14	–0.196	0.016	0.070	Head to pelvic fin
2–3	–0.215	0.009	0.141	Head to dorsal fin
3–16	–0.209	0.145	0.073	Dorsal to pectoral fin
3–14	–0.207	**0.301**	0.067	**Body depth**
3–13	–0.198	**0.226**	0.051	**Dorsal to pelvic fin**
3–11	–0.198	0.013	0.052	Dorsal to anal fin
3–6	–0.205	–0.146	0.022	Dorsal to adipose fin
6–13	–0.201	0.015	0.032	Pelvic to adipose fin
6–11	–0.199	0.143	–0.065	Anal to adipose fin
6–8	–0.193	0.085	*0.209*	*Adipose to caudal fin ventral insertion*
6–7	–0.174	–0.013	*0.217*	*Adipose to caudal fin dorsal insertion*
7–11	–0.171	–0.053	0.004	Caudal fin dorsal insertion to anal fin
7–8	–0.206	0.002	0.062	Caudal fin dorsal to caudal fin ventral insertion
8–11	–0.180	–0.052	0.038	Anal fin to caudal fin ventral insertion
11–13	–0.197	–0.057	0.149	Pelvic fin insertion to anal fin insertion
13–16	–0.207	0.038	0.017	Pectoral to pelvic fin
16–17	–0.132	**0.597**	0.144	**Length between premaxilla and pectoral**
1–16	–0.139	–0.175	0.070	Snout to below pectoral
1–17	–0.135	**–0.254**	0.015	**Snout to below premaxilla**
1–18	–0.153	**–0.333**	–0.006	**Snout to orbit**
3–5	–0.155	0.160	*–0.586*	*Dorsal fin length*
10–11	–0.211	–0.023	–0.151	Anal fin height
9–11	–0.166	0.105	*–0.641*	*Anal fin length*
12–13	–0.193	–0.167	–0.050	Pelvic fin length
15–16	–0.135	–0.082	–0.042	Pectoral fin length
A1	–0.254	**–0.309**	–0.134	**Caudal fin area**

Note: Morphometric variables are the distances between the landmarks numbered in Fig. 1. The morphometric variables with important loadings (threshold = 0.2) along PC2 are indicated in bold and along PC3 in italic.

Table 3. Ranges of the mean flow velocity, standard deviation (SD), and minimum and maximum streamwise *U*, vertical *V*, and lateral *W* flow velocity components ($cm \cdot s^{-1}$) under low and high turbulence intensities.

		U	*V*	*W*
Low turbulence intensity (0.22 $cm \cdot s^{-1}$)	Mean	23.01–23.04	–0.04–0.92	0.09–0.10
	SD	5.13–5.15	4.92–5.09	5.41–5.59
	Minimum	5.23–5.64	–27.64 to –21.89	–26.88 to –21.71
	Maximum	34.98–37.58	21.84–29.73	28.19–28.23
High turbulence intensity (0.35 $cm \cdot s^{-1}$)	Mean	23.01–23.04	–0.15 to –0.01	0.29–0.33
	SD	7.99–8.07	7.35–7.56	7.69–7.70
	Minimum	0.17–0.90	–30.32–29.56	–29.61 to –29.76
	Maximum	44.85–46.91	29.52–30.34	29.95–32.45

heads than wild fish. These morphological differences may affect total swimming costs.

Numerous studies have compared the swimming performance of species characterized by large differences in body morphology (Lighthill 1971; Videler 1993; Webb and Gerstner 2000). However, very little is known about the energetic consequences of relatively minor differences in morphometry and shape observed among morphs of a given species. In fact, most studies on swimming performance have focused on steady swimming and fast starts in low-turbulence flumes or still water. Our results were obtained for fish swimming in highly heterogeneous flow. In turbulent water, costs of swimming may require an assessment of the costs of stabilizing the swimming trajectory in the face of turbulence-induced disturbances. There are no data on the energy costs of stabilization. However, maneuvers that dominate routine swimming time activity budgets (Webb 1991; Krohn and Boisclair 1994; Tang et al. 2000) have been argued to represent a mirror image of a behavior aimed at maintaining stability (Webb 2002). Flow visualization shows

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Fig. 3. Velocity time series of 1 min (25 Hz) for the two different flow conditions with a mean flow velocity, $\bar{u}$, of 23 cm·s^{-1} and two standard deviations of the flow velocity, u_{SD}, of (*a*) 5 cm·s^{-1} and (*b*) 8 cm·s^{-1} in the swimming chamber in which juvenile Atlantic salmon (*Salmo salar*) swam during the respirometry experiments.

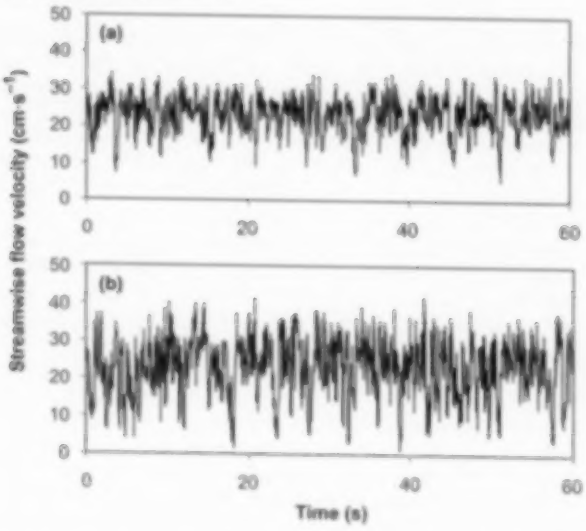
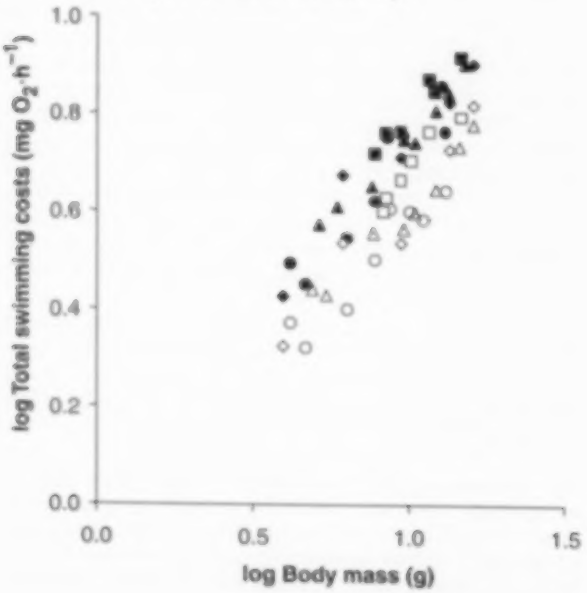
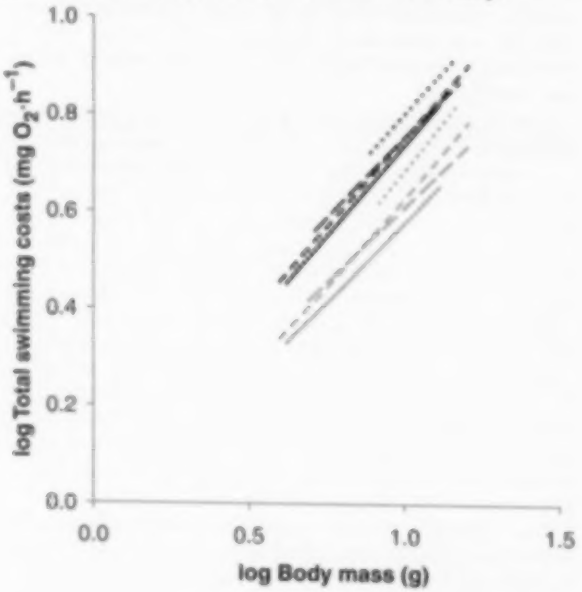


Fig. 4. Total swimming costs of wild fish (●), farmed fish from the Sainte-Marguerite River (▲), farmed fish from the Imsa River (◆), and domesticated fish (■) under low (open symbols) and high (solid symbols) turbulence intensity.



that maneuvers often involve substantial energy losses in vortex rotation (Drucker and Lauder 2003), and hence high induced energy costs are expected. Mechanics and metabolic studies of routine swimming show over tenfold increases in

Fig. 5. Regression lines representing the relationship between body mass and total swimming costs of wild fish (—), farmed fish from the Sainte-Marguerite River (– – –), farmed fish from the Imsa River (- - -), and domesticated fish (……) under low (shaded lines) and high (solid lines) turbulence intensity.



energy costs compared with those expected for rectilinear swimming at the same mean speed (Weatherley and Gill 1987; Webb 1991; Boisclair and Tang 1993). It may be expected that stabilizing swimming postures incur similar energy costs. These could outweigh those of rectilinear swimming, so that explanations for the observed differences in swimming costs may be sought in terms of likely effects of morphology on stability.

Numerous effectors are involved in both maneuvers and stability: the body, median fins including the caudal fin, and the paired fins (Webb 2002). The caudal fin may be particularly important in stability because it is large and lies at a large distance from the centre of mass. In general, stability and maneuverability may be facilitated by large caudal, dorsal, and anal fins providing opportunities for large correction forces and a longer caudal peduncle increasing caudal fin torques (Weihs 2002). Larger body depth may reduce the tendency to slip, which is an adaptation to reduced steady swimming costs, but may add to correction costs following a disturbance (Lighthill 1971). Thus, stability is expected to improve as values become smaller for both PC2 and PC3. As a result, wild fish with the most negative values of PC2 and PC3 (smaller body depth and larger fins) may be expected to have the lowest stability costs and hence the lowest swimming costs in turbulent flow. The farmed JAS from the Sainte-Marguerite River with large tails but smaller dorsal and anal fins would be expected to have reduced stability and swimming costs higher than those of the wild fish. Similarly, higher swimming costs of farmed JAS of the Imsa River compared with wild JAS are consistent with intermediate-sized tails. Domesticated JAS with the highest swimming costs had the

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largest positive values for PC2 and hence smaller tails and large body heights. Our observations suggest that these characteristics may have the largest consequence on the control of stability and on energetic costs of swimming in turbulent flow. Although there is uncertainty in matching shape and stability, arguments based on the costs of stability may provide the most coherent hypothesis to explain the observed variations in swimming costs among wild, farmed, and domesticated JAS.

Total swimming costs varied with turbulence intensity and among the four groups of fish. The total swimming costs increased by an average factor of 1.4 as standard deviation of the flow velocity increased from 5 to 8 cm·s^{-1} and as turbulence intensity increased from 0.22 to 0.35. Furthermore, total swimming costs increased with body mass. The effect of body mass and mean flow velocity is well established and is included in all swimming costs models currently available (Beamish 1978; Brett and Groves 1979; Farrell et al. 2003). However, our results indicated that descriptors of flow turbulence such as the standard deviation of the flow velocity or the turbulence intensity may be required to adequately estimate the total swimming costs under turbulent flow conditions. JAS live in gravel-bed rivers characterized by highly turbulent flow. Estimates of swimming costs derived from experiments with minimized flow heterogeneity, such as forced swimming models, may therefore underestimate the actual cost of swimming of JAS in their natural environment. Enders et al. (2003) estimated the magnitude of the effect of turbulence on fish respiration rates by comparing the swimming costs incurred by fish under turbulent flows with those predicted by the forced swimming model of Boisclair and Tang (1993). This analysis indicated that forced swimming models might underestimate swimming costs in turbulent flows by a factor ranging from 2 to 4. Such comparative analysis cannot be performed with the results of the present study because the models of Boisclair and Tang (1993) were developed to estimate net swimming costs (total respiration rate of unfed fish minus the standard metabolic rate of fish). In the present study, we estimated only the total swimming costs of unfed fish. Comparisons between total swimming costs and net swimming costs would be misleading. Calculations of net swimming costs from our data would have required an estimate of standard metabolic rate (SMR) for each fish group. Because such data do not exist for the four fish groups studied and because SMR may vary among fish of different origins within a species (Boily and Magnan 2002; Grisdale-Helland et al. 2002; Trudel et al. 2004), we did not perform the calculation of potentially misleading net swimming costs for our four fish groups. Consequently, in the present study, we estimated the magnitude of the effect of turbulence on fish respiration rates by developing a new forced swimming costs model. This model was based on the data set used by Boisclair and Tang (1993) with the exceptions that the dependent variable was not net swimming costs but total swimming costs and that temperature was added as an independent variable. Indeed, before developing their model, Boisclair and Tang (1993) subtracted from published total swimming costs the SMR values provided in the papers they used to perform the empirical analysis. Hence, the development of a new forced swimming model (forced total swimming costs (FTSC), mg O_2·h^{-1}) simply required the reversal of the computational approach used by Boisclair and Tang (1993). This procedure resulted in the development of the following FTSC model

$$\log_{10}\mathrm{FTSC} = 0.96\log_{10}M + 0.23\log_{10}\bar{u} + 0.67\log_{10}T - 1.85 \quad (2)$$

where FTSC is the total swimming costs under minimized flow heterogeneity (mg O_2·h^{-1}), M is the body mass of fish (g wet), $\bar{u}$ is the mean flow velocity (cm·s^{-1}), and T is the water temperature (°C). Body mass explained 79% of the variance in the FTSC model ($F_{[3,114]} = 162.35$, $R^2 = 0.81$, $p < 0.0001$). The new FTSC model predicted that the total swimming costs of a 10-g fish swimming at a speed of 23 cm·s^{-1} in a flow with minimized flow heterogeneity characterizing forced swimming experiments and at a water temperature of 15 °C should be 1.58 mg O_2·h^{-1} (95% confidence intervals: 1.35–1.85 mg O_2·h^{-1}). The total swimming costs that we estimated for 10-g wild JAS swimming against our low and high turbulence intensities were, respectively, 2.4-fold (3.80 mg O_2·h^{-1}) and 3.5-fold (5.55 mg O_2·h^{-1}) higher than predicted by the FTSC model (Table 4). Differences between the predictions by the FTSC model and our observations were more pronounced for domesticated JAS, ranging from 3.1-fold (low turbulence intensity, 4.91 mg O_2·h^{-1}) to 4.0-fold (high turbulence intensity, 6.31 mg O_2·h^{-1}). Observations on fish behavior suggested that swimming in a turbulent flow should increase the swimming costs of fish (McLaughlin and Noakes 1998; Pavlov et al. 2000). Our study therefore supports the suggestion that total swimming costs in flow of fluctuating velocities are 2.4- to 4.0-fold higher than in steady flow conditions.

Our results indicated that total swimming costs of wild and farmed JAS were not significantly different. We therefore conclude that swimming costs models obtained using farmed fish can be employed to estimate the swimming costs of wild fish. However, total swimming costs of wild and farmed JAS differed significantly from the total swimming costs of domesticated JAS. The differences were larger between wild and domesticated JAS (15.2% to 29.2%) than between farmed and domesticated JAS (12.5% to 16.2%). These results suggest that swimming costs models developed with wild or farmed fish should not be applied to domesticated fish, and vice versa.

The observed morphometric differences among the four fish groups may not be the only explanation for the differences in the total swimming costs. Three alternate hypotheses might explain the observed difference between the total swimming costs of wild and domesticated JAS.

First, this difference may result from a conditioning effect. Throughout their freshwater life, wild JAS are exposed to turbulent flow with mean focal point velocities of 5–40 cm·s^{-1} (DeGraaf and Bain 1986). When feeding on invertebrate drift, fish are exposed to even higher mean flow velocities of 10–120 cm·s^{-1} (Morantz et al. 1987). Therefore, wild JAS may be better conditioned to swim against the experimental flow than farmed or domesticated fish. Conditioning improves growth rate and food conversion efficiencies and changes condition factor and body composition (see Davison (1997) for a review). JAS increased their sprint performance when exposed to flows of 1–2 body

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Table 4. Total swimming costs and 95% confidence intervals (in parentheses) of 10-g fish under two turbulence intensities characterized by the same mean flow velocity of 23 cm·s^{-1} and two different standard deviations of 5 cm·s^{-1} and 8 cm·s^{-1}.

	Group 1	Group 2	Group 3	Group 4
Total swimming costs (mg O_2·h^{-1}) under low turbulence intensity	3.80 (3.41–4.24)	4.14 (3.91–4.38)	4.32 (3.54–5.26)	4.91 (4.62–5.22)
Factor A	2.4	2.6	2.7	3.1
Total swimming costs (mg O_2·h^{-1}) under high turbulence intensity	5.55 (4.91–6.27)	5.70 (5.48–5.93)	5.65 (4.74–6.73)	6.39 (6.13–6.66)
Factor B	3.5	3.6	3.6	4.0

Note: Four fish groups were compared: (1) wild fish, (2) farmed fish from the Sainte-Marguerite River, (3) farmed fish from the Imsa River, and (4) domesticated fish. Observed total swimming costs were compared with predictions of a new forced swimming model developed. Factor A represents the factor by which the predictions of the forced swimming model underestimated observed total swimming costs under low turbulence intensity, and factor B is under high turbulence intensity.

lengths (BL)·s^{-1} (McDonald et al. 1998). Unconditioned JAS sustained swimming for 231 s in a flow of 38 cm·s^{-1} (5–8 BL·s^{-1}), whereas fish conditioned to 1 BL·s^{-1} sustained swimming for a longer period of 294 s, and fish conditioned to 2 BL·s^{-1} sustained swimming for an even longer period of 324 s. Our findings that total swimming costs of wild JAS are lower than those of domesticated fish, regardless of the turbulence intensity, are consistent with the hypothesis that conditioning may have provided an advantage to wild fish. However, farmed JAS from the Imsa River and domesticated JAS were raised and held in flow tanks characterized by identical flow velocities. Hence, despite similar conditioning, total swimming costs of farmed fish were significantly different from those of domesticated fish. In addition, although wild and farmed fish experienced different conditioning, we found no significant difference between total swimming costs for these two groups of fish. These comparisons suggest that variables other than conditioning may play a more important role in determining swimming costs. This interpretation is supported by our observation that none of the fish from the four groups was fatigued or exhausted by the experimental conditions. JAS of all groups seemed to be physically capable of swimming continuously over a 6-h period. In their natural environment, JAS likely swim against turbulent flow during shorter time periods to attack invertebrate drift, to explore habitat, or to defend their territory. Therefore, the duration of the experiment may be seen as energetically demanding for the fish. Despite the high demand, fish from the four groups did not show any signs of exhaustion, such as drifting back against the downstream grid. Furthermore, we did not observe a relationship between C_D and time since the beginning of the experiment ($0.00 < r^2 < 0.19$, $0.22 < p < 1.00$). Hence, our experimental conditions did not appear to cause significant fatigue to any of the fish groups during the experiment.

Second, differences in total swimming costs among fish groups may be due to differences in body composition among these groups (Kleiber 1975). Differences in body composition may be related to differences in diet among the fish groups studied. Although we have no data regarding the body composition of the fish studied, it may be hypothesized that this trait differed between wild and farmed or domesticated fish owing to differences in diet: wild fish were fed natural preys items, whereas farmed and domesticated fish were fed with commercial diets. This hypothesis is supported by the study of McDonald et al. (1998), who found 2.2 times higher lipid concentrations in aquaculture JAS than in wild JAS. We are not aware of any study investigating the difference in lipid concentrations between farmed and domesticated JAS. Adipose tissue is metabolically inert relative to lean tissue and does not significantly contribute to the overall metabolism (Hayward 1965). As such, we would expect individuals with high lipid concentrations to have lower mass-specific standard metabolic rates than lean individuals. The results of our study are contrary to the expectation based on the effect of body composition on standard metabolic rate. We observed the highest mass-specific total swimming costs in domesticated, presumably more lipid rich, JAS. Although it is difficult to predict the effect of body composition on mass-specific total respiration rate, another argument suggests that body composition may have played a relatively minor role in our study. Farmed and domesticated fish were held under the same rearing conditions during their entire lives and they were fed the same diet. This suggests that they should have similar body composition. Yet, the farmed fish had mass-specific total respiration rates significantly lower than those of domesticated fish, and the farmed fish (presumably high fat composition) had mass-specific total respiration rates similar to those of wild fish (presumably low fat composition). Hence, body composition may not have had a large effect in our study.

Finally, it may be hypothesized that differences in total swimming costs among the four groups of JAS may be due to SMR that differ among these groups. Variations of SMR between different fish species have been well established (Herrmann and Enders 2000; Steffensen 2002). Trudel et al. (2004) demonstrated that SMRs might also vary, depending on body mass and water temperature, from 0% to 200% among closely related species of Pacific salmon (*Oncorhynchus* spp.). However, only a few studies considered within-species variation of SMR. Boily and Magnan (2002) concluded that there was a statistically significant difference between the SMR of brook charr (*Salvelinus fontinalis*) having different body shapes. Their work does not provide the data required to quantify the magnitude of the difference between fish having different body shapes. Hence, our data do not allow us to reject the hypothesis that SMR variations among the four different groups of JAS may have influenced the total swimming costs.

The observed higher total swimming costs of domesticated JAS may result in higher costs of habitat utilization and ultimately reduce survival rate of domesticated JAS

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once they have escaped into a natural environment. Our study may provide additional support for the suggestion that the invasion of escaped domesticated salmon in natural environments may not only increase the competition for natural resources, but also result in a change in the fitness of wild populations through a decrease in swimming efficiency in turbulent flow if interbreeding occurs.

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Variation in freshwater growth and development among five New England Atlantic salmon (*Salmo salar*) populations reared in a common environment[1]

Mariska Obedzinski and Benjamin H. Letcher

Abstract: We examined phenotypic variation in growth and development from the eyed-egg stage to the age-1+ smolt stage among five New England populations of Atlantic salmon (*Salmo salar*: East Machias, Narraguagus, Sheepscot, Penobscot, Connecticut) reared in a common laboratory environment. Study populations originated from rivers varying in size, latitude, and level of hatchery supplementation and included one reintroduced population (Connecticut was a recipient of Penobscot origin stock). Phenotypic trait differences were found among populations, and the degree of stock variation depended on ontogeny. Eggs were smaller and hatched sooner in the Penobscot (a northern, intensively managed population), but no stock differences were detected in size or growth efficiency from the onset of exogenous feeding to age 0+ summer. Differences again emerged in age 0+ autumn, with the degree of bimodality in length–frequency distributions differing among stocks; the Connecticut had the highest proportion of upper-mode fish and, ultimately, age-1+ smolts. Although genetic effects could not be entirely separated from maternal effects for egg size variation, it is likely that differences in hatch timing and smolt age had a genetic basis. Early emphasis on age-1+ hatchery-reared smolts in the Connecticut may have led to divergence in smolt age between the Penobscot and Connecticut populations in less than eight generations.

Résumé : Nous avons déterminé la variation phénotypique de la croissance et du développement depuis le stade de l'oeuf à yeux apparents jusqu'au stade de saumoneau d'âge 1+ chez cinq populations de Nouvelle-Angleterre du saumon atlantique (*Salmo salar*; East Machias, Narraguagus, Sheepscot, Penobscot, Connecticut) élevées dans le même environnement de laboratoire. Les populations à l'étude proviennent de rivières qui varient en taille, en latitude et par l'importance de l'empoissonnement de pisciculture; une des populations est une réintroduction (la population de la Connecticut a reçu des poissons du stock de la Penobscot). Il y a des différences dans les caractères phénotypiques d'une population à l'autre et l'importance de la variation du stock change en fonction de l'ontogénie. Les oeufs sont plus petits et éclosent plus tôt dans la Penobscot (une population nordique fortement aménagée), mais il n'y a pas de différences entre les stocks quant à la taille et l'efficacité de la croissance depuis le début de l'alimentation exogène jusqu'à l'été de l'âge 0+. Des différences apparaissent de nouveau entre les stocks chez les poissons d'âge 0+ en automne dans l'importance de la bimodalité de la distribution de fréquence des longueurs; la population de la Connecticut possèdent le plus grand pourcentage de poissons du mode supérieur et, en fin de compte, le plus grand nombre de saumoneaux d'âge 1+. Bien que les effets génétiques ne peuvent être entièrement séparés des effets maternels en ce qui a trait à la variation en taille des oeufs, il est probable que les différences dans les moments de l'éclosion et l'âge des saumoneaux aient des bases génétiques. La dominance précoce des saumoneaux d'âge 1+ provenant de pisciculture dans la population de la Connecticut peut avoir mené à une divergence dans l'âge des saumoneaux entre les populations de la Penobscot et de la Connecticut en moins de huit générations.

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M. Obedzinski.[2,3] Department of Natural Resources Conservation, University of Massachusetts, Amherst, MA 01003, USA, and US Geological Survey/Biological Resources Division, S.O. Conte Anadromous Fish Research Center, P.O. Box 796, One Migratory Way, Turners Falls, MA 01376, USA.
B.H. Letcher. US Geological Survey/Biological Resources Division, S.O. Conte Anadromous Fish Research Center, P.O. Box 796, One Migratory Way, Turners Falls, MA 01376, USA.

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[2]Corresponding author (e-mail: mobedzinski@ucdavis.edu).
[3]Present address: University of California Cooperative Extension, Sonoma County, 133 Aviation Boulevard, Suite 109, Santa Rosa, CA 95403, USA.

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Introduction

Management at the population or "stock" level is recognized as an important means of protecting salmonid species. Precise homing to natal spawning streams (Solomon 1973) has led to adaptation to localized environments (Riddell and Leggett 1981; Thorpe and Mitchell 1981; Beacham and Murray 1987) and genetically differentiated populations within and among specific drainages (Riddell et al. 1981; Verspoor 1997). The use of molecular genetics as a tool for differentiating stocks has allowed for fine-scale genetic distinction within and among drainages (Martinez et al. 2000; Beacham et al. 2001; King et al. 2001) and has been critical in determining the degree of reproductive isolation among populations. However, in addition to comparisons at the molecular level, understanding among-population phenotypic differences and the genetic and environmental factors responsible for phenotypic variation is also important for shaping stock-enhancement strategies and reintroductions.

Common environment experiments have been used to separate environmental and genetic components underlying phenotypic variation among populations of many species (Conover and Schultz 1995). By rearing organisms under the same environmental conditions and controlling for maternal effects, it can be inferred that phenotypic differences are attributable to genetic variation (Falconer 1989). In addition to serving as a tool to help evaluate the discreteness of populations, common environment experiments can provide information about expression of fitness-related traits and, when compared with characteristics of the environments of origin, can help to determine whether populations have adapted to local environments. In salmonids, common environment studies have been used to help understand the adaptive basis of intraspecies variation in early life stage development, growth, and survival (Hendry et al. 1998; Kinnison et al. 1998; Haugen and Vollestad 2000), morphology (Riddell and Leggett 1981; Taylor and McPhail 1985), behavior (Swain and Holtby 1989; Taylor 1990), and life history (Quinn et al. 2000; Kinnison et al. 2001).

Two considerations are important when evaluating differences among populations using a common environment approach. First, because the level of selection acting on traits may vary with ontogeny (Stearns 1992), it is important to examine traits over a range of life stages. If the degree of stock variation changes throughout the life cycle, comparisons at one life stage may lead to very different conclusions than comparisons at a different life stage. Second, because many salmonid populations are currently and (or) historically influenced by hatchery supplementation, the effect of artificial selection on both environmental and genetic factors responsible for shaping phenotypes should be considered. Rapid evolution through artificial selection has been demonstrated for many life stages of fish species (Haugen and Vollestad 2001; Conover and Munch 2002; Heath et al. 2003) and may strongly influence variation among salmonid populations.

Molecular DNA analyses comparing Atlantic salmon stocks in North America provide evidence that genetic differences exist among US populations (King et al. 2000; Martinez et al. 2001; Spidle et al. 2003). However, few studies have quantified phenotypic traits among US populations, and further studies are needed to determine whether among-population phenotypic differences have a genetic basis. In this study, we examined phenotypic variation in early growth and development among five New England stocks of Atlantic salmon (*Salmo salar*) reared in a common laboratory environment. To test whether stock variation remains constant throughout the freshwater phase of juvenile salmon, a suite of size and developmental traits was monitored from the eyed-egg stage through to age 1+ spring. To evaluate the extent of natural and artificial selection acting on the expression of juvenile traits, the populations chosen for comparison originated from rivers varying in size, latitude, and level of hatchery supplementation. In combination with observations of wild phenotypes and environmental data, the results of this study could be used to augment inferences regarding stock variation based solely on molecular genetics.

Materials and methods

Study populations

Five US Atlantic salmon populations were chosen for comparison: East Machias (EM), Narraguagus (NG), Sheepscot (SH), Penobscot (PN), and Connecticut (CT) (Fig. 1). The East Machias (drainage area 650 km^2), Narraguagus (782 km^2), and Sheepscot (591 km^2) are small coastal watersheds (Baum and Jordan 1982; Dube and Fletcher 1982; Meister 1982), whereas the Penobscot (22 196 km^2) and Connecticut (29 000 km^2) are the two largest Atlantic salmon watersheds in the United States (Baum 1983; Rideout and Stolte 1989). The mouth of the East Machias River is the furthest north and east (44°43′33″N, 67°19′52″W), and the Connecticut River is the furthest south and west, entering salt water at 41°16′26″N and 72°22′12″W.

The five study populations have experienced varying levels of hatchery supplementation, ranging from river-specific fry stocking to complete reintroduction. The East Machias, Narraguagus, and Sheepscot stocks have been managed less intensively than the Penobscot and Connecticut stocks, especially during recent years. In 1992, management practices on these three rivers shifted from stocking fish of mixed origin (predominantly PN, NG, and Machias strains; Baum 1997) to a river-specific stocking program. Under this program, parr are collected from their respective rivers of origin and reared in river-specific isolation to maturity at US Fish and Wildlife Service Craig Brook National Hatchery (CBNFH) in East Orland, Maine, USA. Progeny are stocked primarily as fry into their respective rivers (Baum et al. 1992). All adult returns spawn naturally in these rivers.

The PN and CT stocks represent intensively managed populations in this study. The Penobscot River was historically stocked with fish of mixed origin (Penobscot River, other US rivers, and Canadian rivers) until 1991 when management practices shifted to river-specific stocking (Baum 1997). The native CT population was extirpated in the late 1700s, and between 1967 and 1994, salmon were reintroduced from other North American stocks, predominantly the PN (Rideout and Stolte 1989). Under current practices on both rivers, a portion of river-specific sea-run returns (90% CT, and 21% to 93% PN, annually since 1992) along with domestic river-specific broodstock (F_1) are used for producing fry, parr, and smolts that are stocked into the respective

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Fig. 1. Map of five New England (USA) study population drainages: East Machias (EM), Narraguagus (NG), Sheepscot (SH), Penobscot (PN), Connecticut (CT).

rivers (USASAC 2003). Hatchery influence is probably greater in the CT population than in the PN as the mean annual number of sea-run returns allowed to spawn naturally in the CT drainage since 1992 is approximately 21 compared with 792 in the PN drainage (USASAC 2003).

Current population sizes for all of the study rivers are only a fraction of historical estimates for US rivers (Colligan et al. 2002). Based on recent low adult returns (USASAC 2003), the EM, NG, and SH are listed as "endangered" under the Endangered Species Act.

Egg collection

In January and February 2002, eyed eggs from the EM, NG, SH, PN, and CT populations were obtained from federal hatcheries and transported in water coolers to the US Geological Survey Conte Anadromous Fish Research Center (CAFRC) in Turners Falls, Massachusetts, USA, where they were reared under common laboratory conditions. Collections were made from families spawned between 13 and 16 November 2001, which was approximately the peak spawn time for broodstock from all five hatchery populations. Eggs from the EM, NG, and SH were obtained from CBNFH and were offspring of 4- and 5-year-old female broodstock, collected as age-1+ or age-2+ wild parr in 1998, spawned with 6- and 7-year-old males, collected as parr in 1996. PN eggs, obtained from US Fish and Wildlife Service Green Lake National Fish Hatchery in Ellsworth, Maine, USA, and CT eggs, obtained from US Fish and Wildlife Service White River National Fish Hatchery in White River, Vermont, USA, were offspring of 3- and 4-year-old F_1 broodstock. Four thousand eggs were collected for each stock. The EM, NG, and SH were each represented by equal numbers of 14 full-sibling families, whereas the CT and PN represented random samplings of 100 (CT) or 300 (PN) full-sibling families. EM, NG, and SH eggs were transported to CAFRC on 18 and 23 January, PN eggs on 31 January, and CT eggs on 15 February. Before arrival at CAFRC, the EM, NG, SH, and PN eggs had experienced a similar number of degree-days (calculated by summing the mean daily temperatures since spawning) and were placed in separate trays of a common vertical stack incubator set at an initial temperature of 1.5 °C. CT eggs had experienced fewer degree-days upon arrival at CAFRC and were therefore placed in a separate, warmer (4 °C) incubator for 2 weeks before being transferred to the common, colder incubator containing the other four stocks. Although it is possible that placing the CT eggs in warmer water could have affected egg size, we decided that increasing the temperature of the CT population by 2.5 °C for 2 weeks (<10% of incubation period) was probably less of a concern than the potential effect of a difference in degree-days on hatch timing, which has a well-documented relationship with incubation temperature (Murray and McPhail 1988; Beacham and Murray 1990). Once all five stocks were in the common egg bank, incubation temperatures were designed to approximately mimic trends experienced in the rivers, averaging 1.5 °C through March and then increasing to 13 °C by mid-May (Fig. 2). Water was semi-recirculating with a turnover rate of 0.6 $L \cdot min^{-1}$ and replacement time of ~7 h. Light was eliminated (except during sampling) by covering the trays with black plastic. All mortalities were counted and removed daily. In February, once all stocks had experienced the same number of degree-days (CT was caught up), 20 eyed eggs from each stock were preserved in 10% formalin. Preserved eggs were subsequently placed in a drying oven at 60 °C for 7 days and were individually weighed to the nearest 0.1 mg.

Experimental design

Alevin development and growth

Two hundred and twenty-four eyed eggs from each population were randomly selected from the stock-specific incubation trays and placed into two unoccupied replicate trays (112 eggs per stock per tray) in the same egg bank system. Within each tray, populations were separated into five perforated polyvinyl chloride (PVC) egg cups (10 cm diameter with a mesh bottom and covering) and randomly assigned to a location within the tray. Between 8 March (just before hatching) and 22 April (the end of hatching), the number of hatched eggs in each cup was recorded daily. The number of degree-days from fertilization to hatching was recorded for each egg. For each cup, the number of degree-days to the point when 50% of the individuals hatched (median degree-day) was calculated. On three sampling occasions between hatching and yolk absorption, 20 alevins were removed from each cup, sacrificed, and preserved in 10% formalin. Subsequently, yolk and body tissue were separated by dissection,

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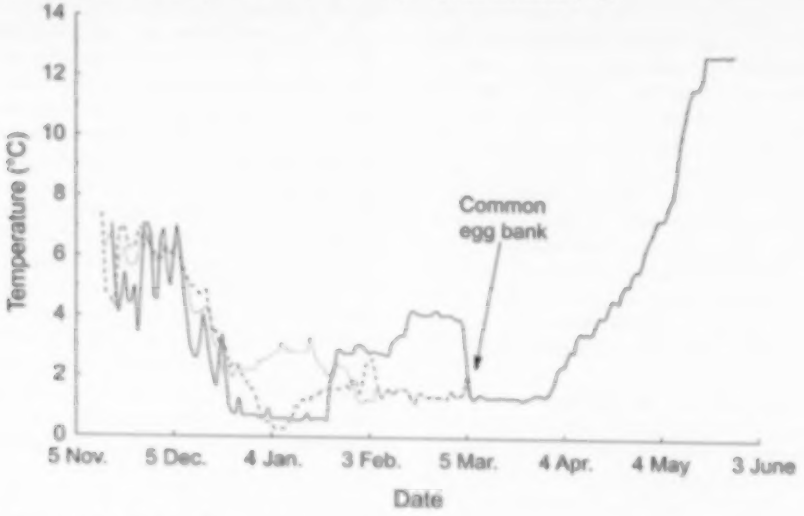
Fig. 2. Incubation temperatures for five populations of Atlantic salmon (*Salmo salar*) reared from November 2001 until May 2002. Stocks: East Machias, Narraguagus, and Sheepscot (···); Penobscot (- - -); Connecticut (—).



dried at 60 °C for 4 days, and individually weighed to the nearest 0.1 mg.

Early parr (age-0+) size/growth

In late May, 1500 unfed fry from each stock were divided into three lots and randomly assigned to three stock-specific 25-L tanks (total of 15 tanks, three replicate tanks per stock). A common semi-recirculating system kept the water at a mean (±1 standard deviation (SD)) temperature of 17.3 ± 0.8 °C, flow of 3.2 ± 0.1 L·min^{-1}, and water replacement time of ~4 h. Artificial lights were timed according to natural photoperiod. To control for density, mortalities in each tank were recorded daily, and full tank counts were conducted each month. Each week, similar-sized "filler" fish were added to the tanks to replace mortalities. Replacement fish were marked with a fin clip so that they could be distinguished from study fish and not used for data collection. As fish grew, densities were adjusted to 300 (28 June), 220 (30 July), and 120 (7 September) by removing equal numbers of randomly selected fish from each tank. Fish in each tank were fed the same amount of commercial dry feed by hand once or twice daily. Between May and mid-August, dry feed was supplemented with *Artemia franciscana* nauplii once daily (equal volumes of known density per tank). On five occasions between June and October 2002, 30 individuals from each tank were randomly selected, anesthetized using $NaHCO_3$-buffered tricaine methanosulfate (MS-222), and sampled for fork length (±1 mm) and wet mass (±1 mg). The day after each sampling event, one-third of the fish from each tank was mixed with one-third of the fish from the other two replicate tanks of the same stock to reduce the opportunity for persistent tank effects. Each new group was then placed back into one of the three original tanks for that stock.

Early parr (age-0+) growth-efficiency experiments

Two growth experiments were conducted in late June and early August 2002 to compare growth efficiency among the five stocks at four different feeding levels. Feeding levels were based on an estimate of C_{max}, a measure of the maximum amount of food that a fish can eat in 1 day (Elliott 1975), and included 0%, 25%, 50%, and 100% of the estimated C_{max} for juveniles at the time of the experiment. Each population – feeding level combination was replicated for a total of forty 17-L experimental tanks, and 10 fish were placed in each tank for a total of 400 fish in each experiment. Experimental tanks were operated on a common semi-recirculating water system kept at a mean temperature (±1 SD) of 17.0 ± 0.3 °C (June) or 17.3 ± 0.5 °C (August), water replacement time of ~12 h, and under artificial light conditions timed according to natural photoperiod. Flow (±1 SD) into each tank was 0.56 ± 0.04 L·min^{-1}. To eliminate outliers, experimental fish were size-selected from within an 80% confidence interval around the mean for that stock (based on size data). At the beginning of an experiment, fish in each tank were individually fin-marked with alcian blue dye and measured for fork length (±0.1 mm) and wet mass (±1 mg). To estimate initial dry masses for individuals, on the day before an experiment, 15 fish per stock were weighed for wet mass (±1 mg), dried at 60 °C for 48 h, and then weighed for dry mass (±0.1 mg) to develop a wet mass to dry mass regression.

For 10 days (June) or 7 days (August), the fish were fed live *Artemia* nauplii twice daily (1000 and 1400). Within each feeding treatment, equal numbers of *Artemia* per fish were placed in each tank. *Artemia* were quantified by calculating the density of a stock solution each morning using image analysis. At each feeding, the appropriate volume of stock solution was pipetted into each tank based on feeding level and adjusted accordingly for any fish mortality since the previous feeding. In the high food availability tanks, uneaten *Artemia* from the previous day were siphoned from each tank daily and quantified using image analysis. The difference between the number of *Artemia* fed on a given day and the number of *Artemia* recovered the following morning was used as an estimate of the number of *Artemia* consumed

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for each tank on each day. The other treatment tanks were siphoned for a similar period of time to ensure equal disturbance to all tanks.

Approximately 40 h after the final feeding in an experiment, all fish were sampled for fork length (±0.1 mm) and wet mass (±1 mg), and the alcian blue mark was recorded. The fish were then placed in a drying oven for 48 h at 60 °C, and individual dry masses (±0.1 mg) were recorded. To convert the number of *Artemia* consumed into dry-mass values, 125 samples of *Artemia* (quantity ranging from 3200 to 51 200) were pipetted onto fine-mesh Nitex® screening, dried at 60 °C for 24 h, and weighed to the nearest 0.1 mg. The dry mass for a single *Artemia* was calculated for each sample and was then averaged across all samples. This overall mean was multiplied by the estimated number of *Artemia* consumed to give dry-mass values for consumption.

Late parr (age 0+ to age 1+) size distributions

In mid-October, when all of the parr in the 15 tanks used in the early parr comparisons were greater than 60-mm fork length, 120 fish from each population were individually marked by inserting a passive integrated transponder (PIT) tag into the body cavity (Gries and Letcher 2002). To reduce potential agonistic behavior in the tanks, fish were size-selected from within a 60% confidence interval around the mean for that stock. Although this eliminated the possibility of capturing the full range of sizes for each stock reared in a laboratory environment, because the variance in size was the same for all stocks in October (based on length and mass data collected 3 days before tagging), we believe that selecting fish within a 60% confidence interval around the mean affected the size distribution for each stock equally. Tagged fish were divided into four replicate groups of 150 fish, with each replicate containing 30 fish from each of the five stocks. Fish were initially held in four 400-L tanks and then were transferred to four 1000-L tanks in March 2003. Temperatures decreased slowly from 16.5 °C in October to a low of 4.5 °C in March and then increased to 11 °C in May. Throughout the study, fish in all tanks were fed the same amount of commercial dry feed twice daily. All fish were sampled monthly for fork length (±1 mm) and wet mass (±0.01 g) between October 2002 and May 2003.

Data analysis

For all statistical analyses, differences of $p < 0.05$ were considered significant. To test for violation of assumptions of parametric analysis, the Kolmogorov–Smirnov one-sample test for normality, the Brown–Forsythe test for homogeneity of variances, and the test for homogeneity of slopes (analysis of covariance (ANCOVA) models) were conducted on data for all experiments with large sample sizes ($n > 10$). Tukey's honestly significant difference (HSD) was used as a post hoc test for analysis of variance (ANOVA) models.

Alevin development and growth

Stock variation in egg dry mass was assessed using one-way ANOVA. Two-way ANOVA with stock and tray as main factors was used for comparing alevin total dry mass, yolk dry mass, and body tissue dry mass among the five stocks at each of the three samples. ANCOVA with egg dry mass as a covariate was also run to determine whether variation in alevin size was attributable to egg size differences. Growth rate, yolk use rate, and yolk conversion efficiency were compared among stocks for the two intervals between sampling events. Because sampling required sacrificing alevins, the rates and conversion efficiency between two samples were calculated using dry mass averages of 20 sacrificed alevins per cup at each sample, resulting in two observations per stock per interval for growth rate, yolk use rate, and conversion efficiency. Growth rate for each cup of alevins was calculated as the difference in natural logarithms of the average body tissue dry mass at two consecutive samples divided by the difference in degree-days. Similarly, yolk use rate was calculated as the difference in natural logarithms of the average yolk dry mass at two consecutive samples divided by the difference in degree-days. Conversion efficiency was calculated as the difference in average dry body tissue mass between two consecutive samples divided by the difference in average yolk dry mass. One-way ANOVA and ANCOVA (egg size as covariate) were used to compare variation in alevin growth and yolk use rates and yolk conversion efficiencies among stocks.

Variation in degree-day to 50% hatching among the five stocks was evaluated using one-way ANOVA with stock as the main factor and degree-day to 50% hatching in each cup as observations. Additionally, ANCOVA (egg dry mass as covariate) was used to test for the influence of egg size on hatch timing. Variance in degree-day at hatching for each cup was calculated using degree-day at hatching for individuals. Variation in hatch distribution among stocks was then tested using the Brown–Forsythe test of homogeneity of variances.

Early parr (age 0+) size/growth

For each of the five samples, a nested ANOVA design (tank nested within population) was used to test for differences in length and wet mass. Growth rates were calculated for successive intervals between samples using mean wet mass values for each tank. Stock differences in growth rate were tested using one-way ANOVA (one growth rate observation per tank).

Early parr (age 0+) growth efficiency experiments

Relative growth (g) and relative ingestion (i) over the course of each experiment were calculated as

$$g = \frac{M_F - M_I}{((M_F + M_I)/2) \cdot d}$$

$$= \text{mg growth} \cdot \text{mg fish}^{-1} \cdot \text{day}^{-1}$$

and

$$i = \frac{\sum_j^d ((\text{mass eaten on day } j)/\text{NF}_j)}{((M_F + M_I)/2) \cdot d}$$

$$= \text{mg consumed} \cdot \text{mg fish}^{-1} \cdot \text{day}^{-1}$$

where M_F and M_I are the final and initial masses of the fish in each treatment, respectively, d is the number of days of the experiment, and NF_j is the number of fish in the tank on day j (Letcher et al. 1997). Equal consumption by individual fish in a shared tank was assumed. Gross growth efficiency (GGE) for each fish was calculated as $100(g/i)$. To compare growth efficiency among stocks, a separate ANCOVA was

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used for each growth experiment with g as the dependent variable, stock as the main factor, and i as a covariate.

Late parr (age 0+ to age 1+) size distributions

Length–frequency distributions for each stock at each sample were used to compare differences in bimodality among stocks between October and May. To determine which individuals were in the upper or lower modes, a common length cutoff was determined by inspection of a length–frequency distribution of pooled stocks at the May sample. Based on length in May, each fish was then assigned to either the upper or lower mode. A rows by columns G test of independence (Sokal and Rohlf 1995) was used to compare the proportion of fish in the upper mode among stocks. Because fish were individually marked, mode assignments could be retrospectively applied to all previous sampling events. Repeated-measures ANOVA (stock and tank as factors, and length or wet mass as the repeated measure in time) was used to compare stock differences in length and mass within each mode. For each mode, the stock–time interaction was separated (SAS lsmeans slice option; SAS Institute Inc. 1999) to compare stock differences in size within each sampling event. To evaluate differences in the timing of development of a bimodal pattern among stocks, individual t tests were run comparing length of retrospectively assigned upper- and lower-mode fish for each stock at each sample.

Results

The data met the assumptions of normality in 99.7%, homogeneity of variances in 90%, and homogeneity of slopes in 100% of the tests conducted. Of the ANOVAs conducted where an assumption was violated, in only one case was the null hypothesis rejected (stock comparison of lower-mode length in December). We do not think this affected the results because the assumption of normality was violated for only one stock (EM) in one of four replicate tanks.

Alevin development and growth

Egg dry mass differed among populations ($p < 0.001$). Post hoc tests revealed that the PN (41.7 ± 7.7 mg) had significantly lighter eggs than all stocks except the CT (EM = 52.3 ± 7.3 mg, $p < 0.001$; SH = 48.7 ± 7.0 mg, $p = 0.009$; NG = 48.5 ± 7.5 mg, $p = 0.013$; CT = 47.4 ± 5.3 mg, $p = 0.056$).

Egg size influences on alevin size persisted through all alevin samples, with the PN and CT generally weighing less in total alevin dry mass than the other stocks at all three samples (Fig. 3*a*). When egg dry mass was included as a covariate in ANCOVA, no stock differences were detected in total alevin mass at any sample, suggesting that stock variation in total alevin mass was attributable to initial egg size differences. No significant differences were found among body tissue mass using ANOVA except at sample 1 when PN alevins had slightly heavier body tissue than the CT alevins (Fig. 3*b*). When ANCOVA was used, no differences in tissue mass among stocks were detected at any sample. Stocks differed significantly in yolk dry mass at all samples using ANOVA, and at sample 2, only, using ANCOVA (Fig. 3*c*). Therefore, differences in total dry mass appear to be a result of differences in yolk mass rather than body tissue mass.

Fig. 3. Alevin (*a*) total dry mass, (*b*) tissue dry mass, and (*c*) yolk dry mass for two replicates ($n = 20$ alevins per replicate) of five populations of Atlantic salmon (*Salmo salar*) taken on three sampling occasions between hatching and yolk absorption. Stocks: East Machias (···○···), Narraguagus (- -□- -), Sheepscot (–◇–), Penobscot (–▲–), Connecticut (–●–).

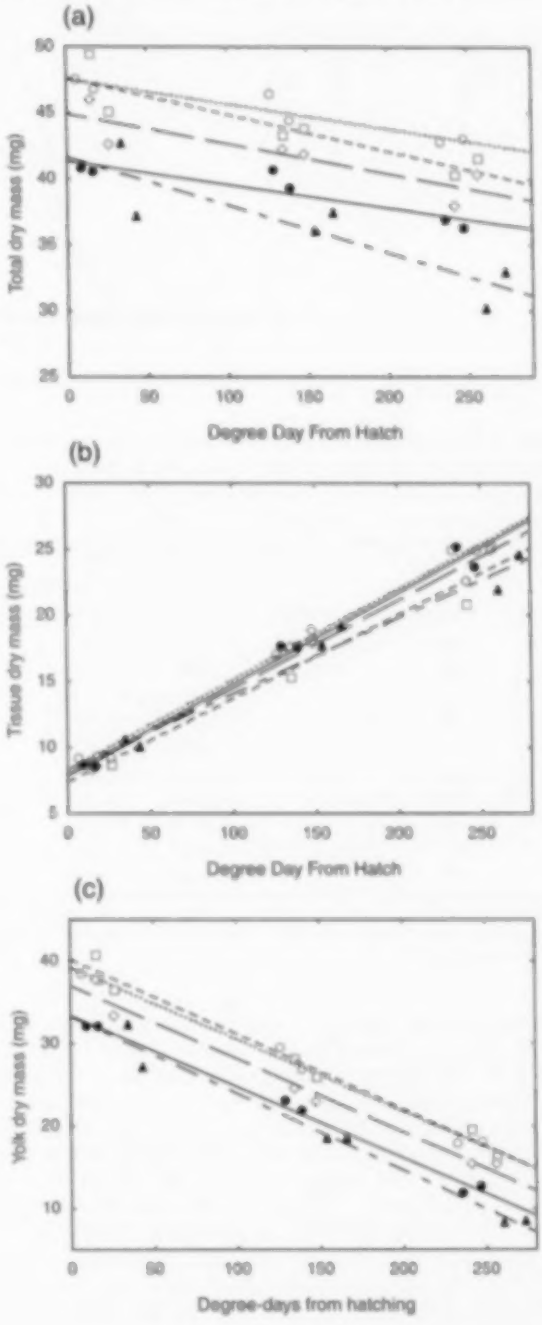

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Fig. 4. Cumulative distribution of hatching by degree-day for two replicates of five stocks reared in a common egg bank. Stocks: East Machias (○), Narraguagus (□), Sheepscot (◇), Penobscot (▲), Connecticut (●).

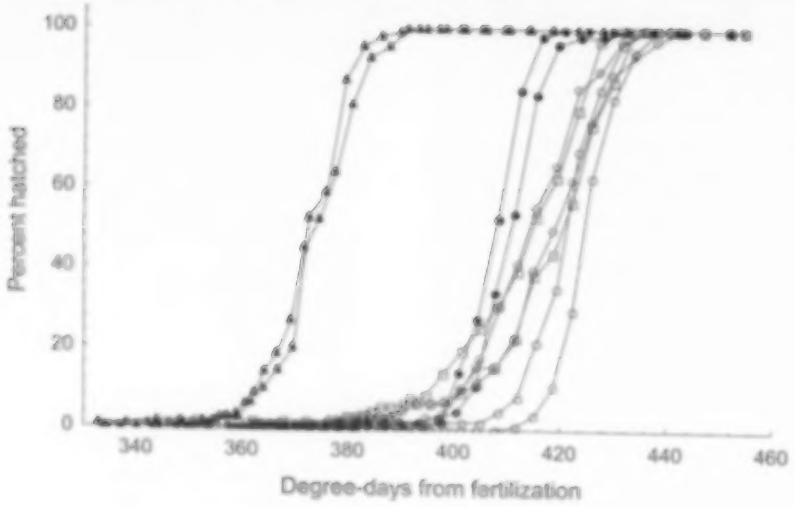

Table 1. Mean (standard error) growth rate, yolk use rate, and yolk conversion efficiency for five populations of Atlantic salmon, *Salmo salar* (n = 2 repetitions per stock), reared in two incubation trays of a common egg bank system.

Interval	Stock	Growth rate	Yolk use rate	Yolk conversion efficiency
1	EM	5.2 (<0.04)	2.5 (0.3)	83 (5)
	NG	5.3 (0.7)	2.9 (0.2)	70 (18)
	SH	6.1 (0.2)	3.3 (0.3)	82 (11)
	PN	4.8 (0.5)	3.9 (0.7)	78 (26)
	CT	5.9 (<0.02)	3.0 (0.2)	93 (6)
2	EM	3.4 (0.2)	4.1 (0.5)	76 (8)
	NG	3.0 (0.1)	3.8 (0.4)	70 (6)
	SH	2.5 (0.2)	4.1 (0.4)	67 (14)
	PN	2.2 (0.1)	7.4 (0.1)	48 (6)
	CT	3.1 (0.3)	5.6 (0.6)	67 (3)

Note: Intervals: 1, 17 April to 7 May; 2, 7 May to 17 May. Stocks: East Machias (EM), Narraguagus (NG), Sheepscot (SH), Penobscot (PN), and Connecticut (CT).

Table 2. Median, mean, and variance in degree-days to hatching for five Atlantic salmon (*Salmo salar*) populations reared in two incubation trays of a common egg bank between March and April.

			Degree-days at hatching		
Stock	Tray	n	Median	Mean	Variance
EM	1	105	423	422	60.7
	2	109	426	427	30.2
NG	1	108	415	414	143.6
	2	107	422	419	218.8
SH	1	110	415	416	104.7
	2	111	419	419	171.2
PN	1	112	373	374	67.4
	2	111	375	375	82.6
CT	1	109	408	409	31.6
	2	111	411	412	66.3

Note: Stocks: East Machias (EM), Narraguagus (NG), Sheepscot (SH), Penobscot (PN), and Connecticut (CT).

Using ANOVA, significant differences in growth rate were found during the growth interval between sample 1 and sample 2; the SH had the highest growth rate, and the PN had the lowest (Table 1). Yolk use rate differed significantly among stocks during both sampling intervals; the PN had the highest yolk use rate during both intervals, the EM had the lowest yolk use rate during interval 1, and the NG had the lowest during interval 2 (Table 1). When egg size was taken into account using ANCOVA, no differences were found in either growth rate or yolk use rate. Using ANOVA or ANCOVA, no significant differences were found in yolk conversion efficiency among stocks during either interval (Table 1).

Hatching timing differed among populations ($p < 0.001$), with PN eggs requiring fewer degree-days to reach 50% hatching (Table 2; Fig. 4) than all other stocks ($p < 0.001$ for each stock compared with PN). CT eggs required fewer degree-days to reach 50% hatching than the EM, NG, and SH stocks, though only significantly fewer than the EM eggs ($p = 0.016$). No differences in hatch time were detected among the EM, NG, and SH ($p > 0.177$ for each two-way comparison). Although a correlation was found between egg size and number of degree-days to reach 50% hatching ($r^2 = 0.92$), when egg size was included as a covariate, the PN still required fewer degree-days than the other stocks to reach 50% hatching ($p = 0.01$). Distribution of hatch timing differed among stocks ($p < 0.001$; Fig. 4) with the variance in degree-day at hatching higher for the NG and SH than the other stocks (Table 2).

Early parr (age 0+) size/growth

No differences in fork length or mass were detected among populations until 16 October when the PN salmon were heavier ($p = 0.038$) and longer ($p = 0.007$) than the EM

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salmon (Figs. 5*a*, 5*b*). Similarly, growth rates did not differ until the September–October interval (length $p < 0.001$, wet mass $p < 0.001$; Fig. 5*c*). During this interval, the EM had significantly slower wet mass growth than all stocks except the CT, and the CT had slower growth than the SH.

Early parr (age 0+) growth efficiency experiments

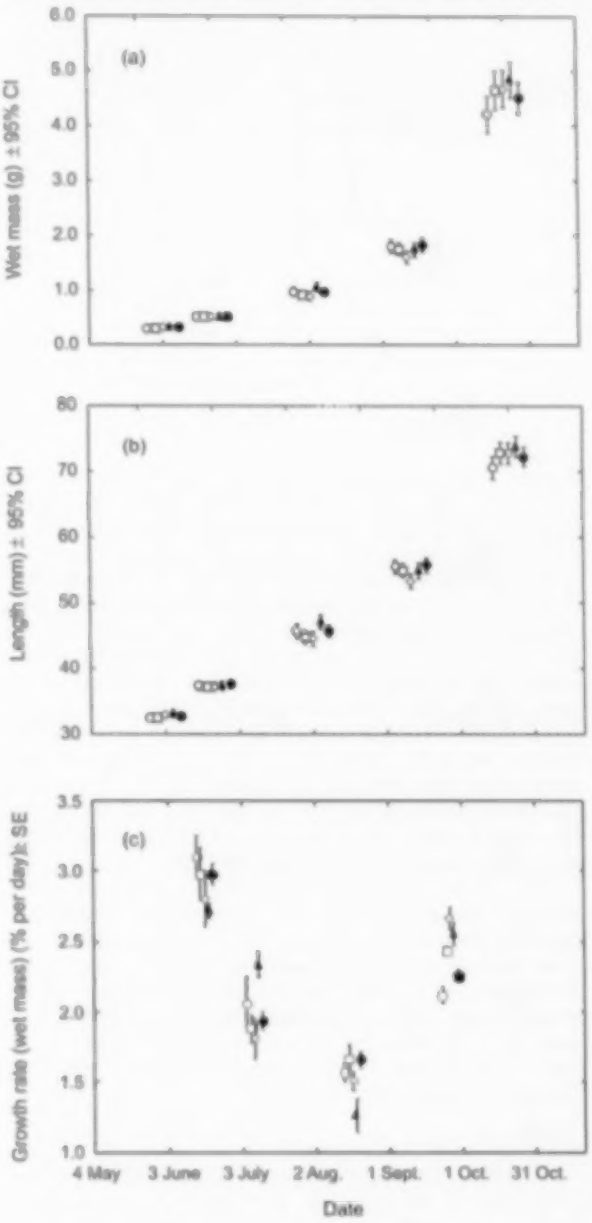
In both June and August experiments, relative growth (g) increased linearly with relative ingestion (i) for all stocks. No differences in growth efficiency were detected among stocks in either June ($p = 0.113$) or August ($p = 0.094$). In both experiments, GGE increased with feeding level, and GGE (means ± 1 SD) across stocks at each feeding level were higher in June than in August (June: 25% C_{max} = 17.8 ± 3.6%, 50% C_{max} = 34.3 ± 1.9%, 100% C_{max} = 39.4 ± 2.0%; August: 25% C_{max} = –34.9 ± 10.5%, 50% C_{max} = 4.2 ± 3.2%, 100% C_{max} = 22.0 ± 2.1%).

Late parr (age 0+ to age 1+) size distributions

In May, the length cutoff separating modes appeared similar for all stocks, so a common breakpoint of 141 mm (Fig. 6) was chosen for separating upper- and lower-mode fish for all stocks. Stock differences were observed in the proportion of fish in the upper mode in May ($p < 0.001$; EM = 11%, NG = 14%, SH = 13%, PN = 21%, CT = 48%; Fig. 7). When the CT was excluded from the row by columns G test, no differences were found among the other four stocks ($p = 0.15$). In comparing retrospectively assigned modal groups within each stock at each sample, t tests indicated that the timing of modal segregation was similar among stocks (Fig. 7). Differences in mean length between upper and lower modes were significant ($p < 0.01$) as early as October for all stocks except the NG ($p = 0.28$). At all subsequent sampling events, differences were detected between modes within each stock ($p < 0.001$ for each stock at each sample).

Repeated-measures ANOVAs testing for stock variation in size revealed differences in length and mass in both upper and lower modes. For length and mass within each mode, overall stock-effect p values were < 0.05, and tank-effect p values were > 0.38. In general, the EM and NG were lighter and shorter than the PN, CT, and SH within each mode (Figs. 8*a*, 8*b*). In the lower mode, stock differences in mass were found in December and at each sample from February through May (Fig. 8*a*), and differences in length were found at every sample from October through May (Fig. 8*b*). In the upper mode, stock differences in mass were found at all samples from February through May (Fig. 8*a*), and differences in length were found at all samples from December through April (Fig. 8*b*).

Fig. 5. Mean (*a*) wet mass, (*b*) length, and (*c*) growth rate (wet mass) for five populations of Atlantic salmon *Salmo salar* (age 0+) on five sampling dates between May and October. Stocks: East Machias (○), Narraguagus (□), Sheepscot (◇), Penobscot (▲), Connecticut (●). CI, confidence interval; SE, standard error.



Discussion

During the first year of life, the level of variation among our five study populations depended on ontogeny. Stock differences were apparent during the egg and alevin stages, undetected during the early parr stage (age 0+ spring to summer), and detected again during the late parr stage (age 0+ autumn to age 1+ spring) (Fig. 9). In the egg and alevin stage comparisons, PN eggs hatched earlier than all other stocks and had smaller eggs than all but the CT stock. Stock differences in mass at the eyed-egg stage persisted throughout the alevin stage until the onset of exogenous feeding. After the fry were stocked into tanks at the end of May, no size differences were detected among stocks until October, when the PN was heavier than the EM. Detailed, individually based growth efficiency experiments conducted in June and August revealed no stock variation in growth ef-

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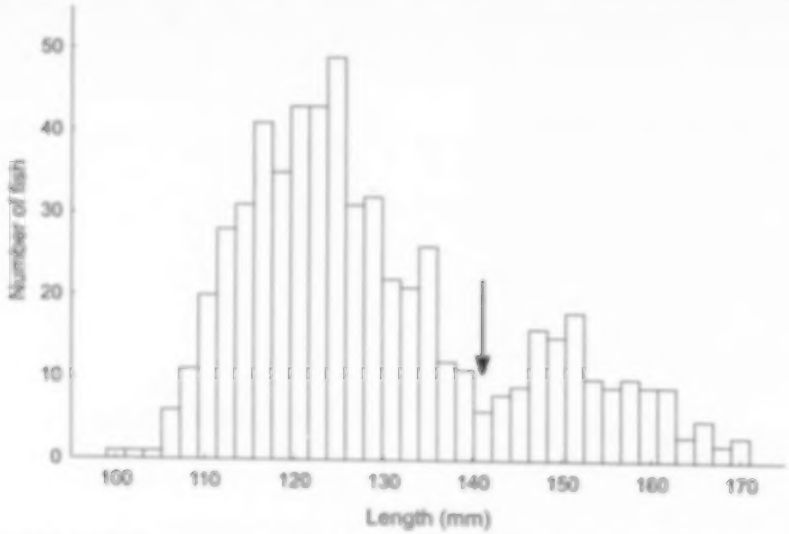
Fig. 6. Length–frequency distribution of pooled stocks in May. Black arrow indicates length cutoff used to divide upper and lower modes for statistical analysis.



ficiency during this period. However, between October and May 2003 (late parr), patterns of bimodality in length–frequency distributions differed among stocks. The proportion of fish comprising the upper mode was higher in the CT (approximately one-half of the fish) than in the other four stocks. At every sample between December and May, stock differences in size were found within each mode, with the EM and NG generally weighing less and having shorter length than the PN, CT, and SH. Over the course of the study, the PN and CT shared a similar overall growth pattern as compared with the other three stocks, with relatively smaller size at the earliest life stages examined and relatively larger size after age 0+ autumn (Fig. 9). In contrast, the overall growth pattern for the EM, NG, and SH showed the reverse trend, with relatively larger size early and smaller size in the later stages of the study.

The results of this study reinforce the importance of examining traits at more than one point in time. Conclusions regarding stock differentiation would have been entirely different had we measured growth characteristics only at the alevin stage, or only between May and September (age 0+ spring through summer). By measuring traits from the egg to smolt stage, we were able to examine sources of stock variation over the portion of Atlantic salmon life history most influenced by management activities.

Alevin size and development

A combination of selection and maternal effects may be contributing to the size and development trait differences found among stocks during the alevin stages in this study. Differences in alevin size, growth, and conversion efficiency were all attributable to differences in egg size as evidenced by the inclusion of egg size as a covariate, resulting in no detectable differences among stocks. The egg–alevin size relationship we found is consistent with that of other studies of juvenile Atlantic salmon (Kazakov 1981; Thorpe et al. 1984) in which larger eggs produced larger alevins and larger unfed fry. Natural and artificial selection pressures may have caused the observed stock differences in egg size; however, because we were unable to obtain eggs for all stocks from the same hatchery, we cannot rule out the possibility that inherited maternal environmental effects are influencing our egg size results. Maternal differences in size (which can be influenced by rearing environment) have been shown to affect egg size (Heath et al. 1999; Kinnison et al. 2001).

In contrast to the results for alevin size, egg size variation could not completely account for differences in hatch timing. Although we found a positive correlation between mean egg mass and degree-day at 50% hatching, even when egg size was included as a covariate, the stock with the smallest-sized eggs (PN) still required significantly fewer degree-days to reach 50% hatching than the other four stocks. The remaining variation in hatch timing could be explained by natural and (or) artificial selection. Temperature differences in incubation environments are a likely source of natural selection; requiring fewer degree-days to hatching is one possible mechanism to compensate for colder incubation environments. Spawning sites in the PN extend further north where temperatures are presumably colder for a longer period of time than in any of the other study drainages. Artificial selection may also be affecting the differences observed in hatch timing. Natural selection against early development caused by predation (Brannas 1995) and extreme flows (Jensen and Johnsen 1999) is reduced in a hatchery environment and may be causing an artificially selected trend towards earlier hatching. In the hatchery, fish that develop faster may get a head start on feeding and establishing a territory without an added mortality risk. If artificial selection is the dominant form of selection acting on hatch timing in these stocks, however, we would expect the CT eggs to hatch at least as early as the PN, given the equally high (or even greater) level of hatchery influence on the CT.

Early parr size and growth

The similarity of size and growth among stocks between May and September (age 0+) suggests that the influence of

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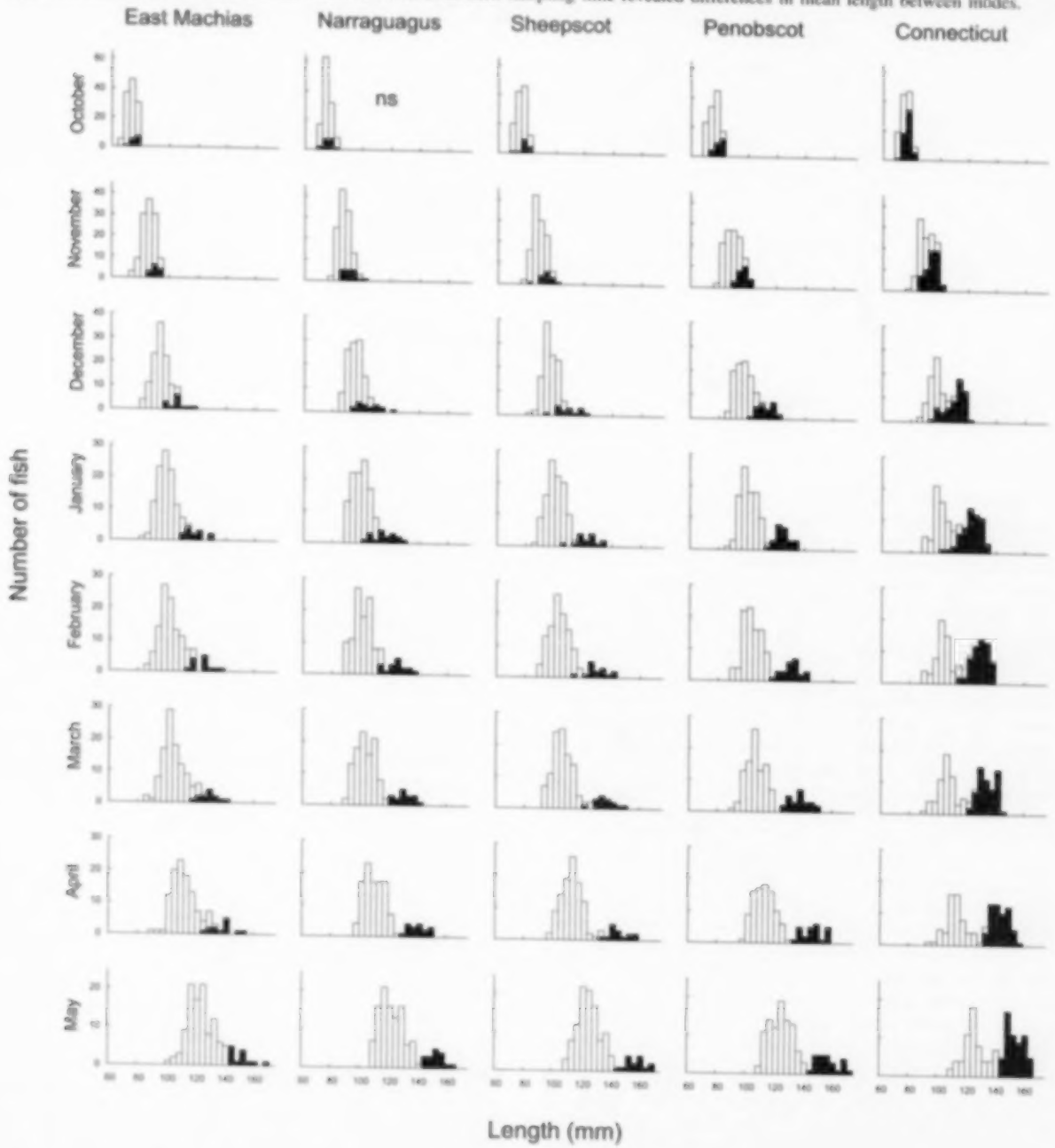
Fig. 7. Length–frequency distributions for each stock at each monthly sample. Fish were divided into modes (open bars, lower mode; solid bars, upper mode) based on a common length cutoff in May (141 mm) and retrospectively assigned that mode at all previous samples. For all stocks at all samples ($p < 0.01$) except the Narraguagus stock in October ($p = 0.28$; ns, not significant), t tests comparing length between upper and lower modes within each stock at each sampling time revealed differences in mean length between modes.



egg size differences on juvenile size and growth did not persist beyond the onset of exogenous feeding. In chinook salmon, Heath et al. (1999) estimated that after about 6 months, the maternal effect on offspring size was not different from zero, and similarly, Thorpe et al. (1984) found that the size advantage of unfed Atlantic salmon fry from large eggs was not maintained through the end of the first growing season under hatchery conditions.

Selection on size during the early freshwater phase of life may be weak in natural stream environments. In a study measuring levels of selection acting on size, condition factor, and growth of juvenile Atlantic salmon introduced as fry

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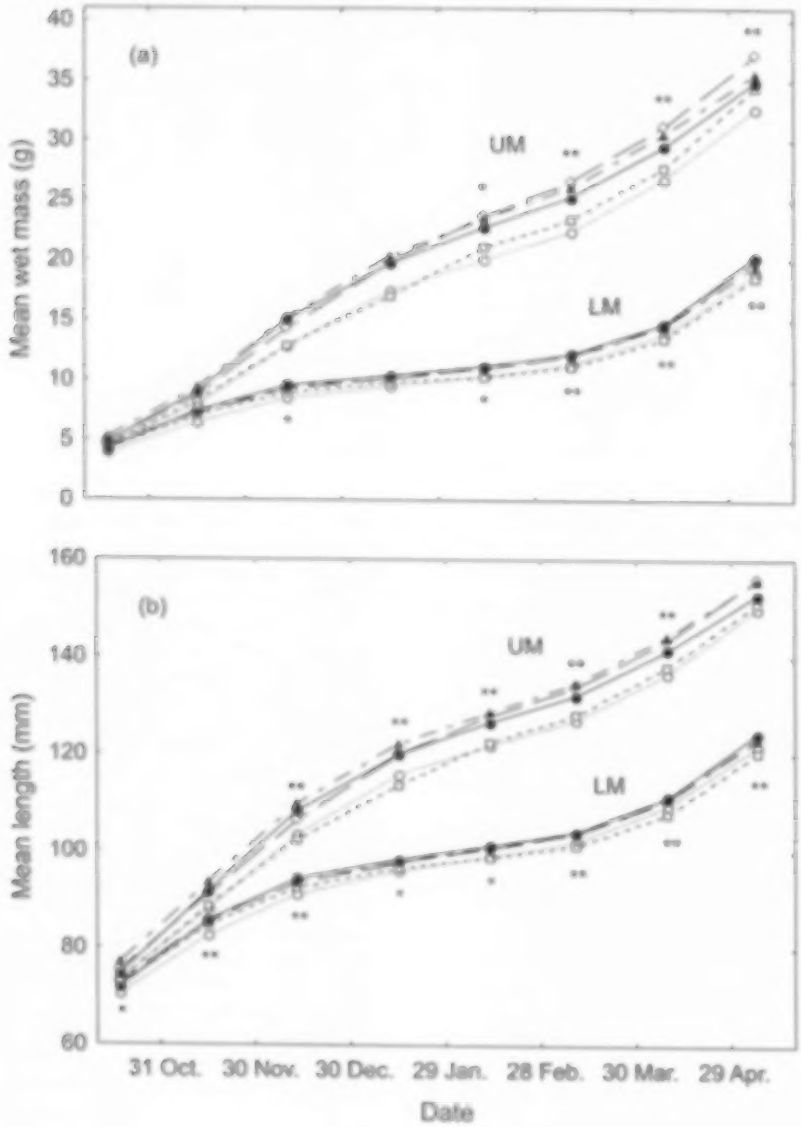
Fig. 8. Mean (*a*) wet mass and (*b*) length for lower (LM) and upper (UM) modes for each stock at each sampling event. Stocks: East Machias (EM; –○–), Narraguagus (NG; - -□- -), Sheepscot (SH; –◇–), Penobscot (PN; –▲–), Connecticut (CT; –●–). Sample sizes: EM, U = 13, L = 105; NG, U = 17, L = 103; SH, U = 15, L = 105; PN, U = 25, L = 94; CT, U = 58, L = 62. Asterisks denote significant differences: $p < 0.05$ (*), $p < 0.01$ (**), $p \geq 0.05$ (ns).



into a tributary of the CT River, Hendry et al. (2003) found little evidence of strong or consistent selection acting on these traits. This was contrary to expectations that (*i*) selection would be high on an introduced population that presumably had not fully adapted to the new environment and (*ii*) that larger fish often have higher survival. If only limited or inconsistent selection on size occurs during the early stages of freshwater experience in the wild, it is not surprising that we detected no among-population differences in length, mass, or growth efficiency at this development stage.

Late parr size distributions

In populations of Atlantic salmon reared in a hatchery environment with favorable growth conditions, bimodal length–frequency distributions typically occur by the first autumn (age 0+ autumn) (Thorpe 1977). The two modes correspond to age at smoltification, with the upper mode smolting at age 1+ and the lower mode smolting at least 1 year later (Thorpe 1977; Thorpe and Morgan 1980; Heggenes and Metcalfe 1991). In our study, bimodal length–frequency distributions were apparent in all stocks except

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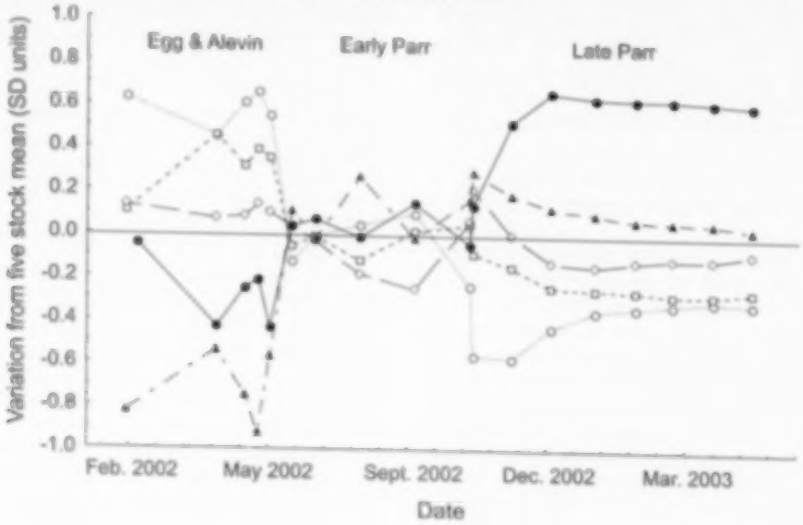
Fig. 9. Size variation among five stocks of Atlantic salmon (*Salmo salar*) between February 2002 and May 2003. At each sampling date, stock means for mass were converted to standard deviation (SD) units from the five stock mean. Stocks: East Machias (···○···), Narraguagus (- -□- -), Sheepscot (–◇–), Penobscot (–▲–), Connecticut (–●–).



the EM by the age 0+ winter (January–February) and were clearly developed in all stocks by age 1+ May. Based on the relationship between length mode and smolt age found in other studies (Thorpe 1977; Thorpe and Morgan 1980; Heggenes and Metcalfe 1991), we are inferring that all upper-mode fish in our study were age-1+ smolts and that the stock differences we found in the proportion of upper-mode fish reflect stock differences in smolt age.

Development of a bimodal size distribution and, in turn, age at smolting is influenced by environmental (Baily et al. 1980; Metcalfe and Thorpe 1990; Nicieza et al. 1991) and genetic (Thorpe and Morgan 1978; Bailey et al. 1980; Nicieza et al. 1994) factors and the interaction between environmental and genetic factors (Thorpe 1977; Stefansson et al. 1990). Because the stocks were reared in a common environment and inherited maternal environmental effects appeared not to influence early parr size, we can infer that the stock variation we observed in age and size at smolting is attributable to genetic variation. While natural and artificial sources of selection are probably both contributing to the differences observed, we suspect that the stock variation we observed in smolt age resulted largely from the different levels of hatchery influence among stocks.

Differences in the life stages used for supplemental stocking and the amount of natural spawning that occurs in the rivers have probably led to varying levels of artificial selection on smolt age among populations. Since reintroduction in the late 1960s, age-1+ smolt stocking has played a large role in Atlantic salmon restoration on the Connecticut River. High levels of age-1+ smolt stocking have also occurred on the Penobscot River (Baum 1997), whereas almost no stocking of smolts has occurred on the East Machias, Narraguagus, and Sheepscot rivers since the early 1990s (USASAC 2003). Under the smolt stocking programs on the Connecticut and Penobscot rivers, hatchery-reared juveniles are size-graded during age 0+ autumn. Lower-mode fish are either stocked out as age-0+ parr or discarded and upper-mode fish are stocked out as age-1+ smolts the following spring. Lower-mode parr stocked at age-0+ parr likely have extremely low survival compared with the fish stocked as age-1+ smolts (Fred Trasko, US Fish and Wildlife Service, Route 180, One Hatchery Way, Ellsworth, ME 04605, USA, personal communication; Jay McMenemy, Vermont Fish and Wildlife Department, 100 Mineral Street, Springfield, VT 05156, USA, personal communication). It is therefore probable that artificial selection for faster-developing fish (age-1+ smolts) has affected the genetic structure of the PN and CT populations. Owing to differences in the amount of natural spawning occurring on the Penobscot and Connecticut rivers, artificial selection has probably had a larger influence on the CT population. In the Penobscot River, a greater number of adult returns originating from naturally spawning adults may be reducing the influence of age-1+ smolt stocking on the composition of this stock. In contrast, in the Connecticut River, almost no natural production has occurred in over 200 years (Rideout and Stolte 1989; USASAC 2003).

The genetic difference in smolt age between the PN and CT is intriguing, as the PN was the primary donor stock for reintroductions to the Connecticut River, which began less than 40 years ago. During the period between 1976 and 1990, approximately 91% of salmon introduced into the Connecticut River were of PN origin (summarized in Martinez et al. 2001), and almost all adult returns were from strains that used at least one PN origin parent (Rideout and Stolte 1989). In approximately eight generations, it appears that genetic differences in smolt age may have arisen between the two stocks. Further supporting this conclusion, a study conducted by Martinez et al. (2001) found differences at both enzyme and microsatellite loci between the PN and CT stocks, although it is possible that these differences were

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the result of genetic drift. Most documented cases of rapid evolution occur in populations that have recently experienced a major anthropogenically caused environmental shift, such as introduction into a new environment (Kinnison et al. 1998; Haugen and Vollestad 2000; Hendry et al. 2000), or removal from the wild into captive breeding environments (Heath et al. 2003). Because the CT population experienced both a new river environment and intense artificial hatchery selection since reintroduction from the Penobscot stock, it is most likely that the CT stock evolved towards an earlier smolt age rather than the PN evolving towards a later smolt age.

Natural selection is another potential source of variation in smolt age among our study stocks. The differences in smolt age we observed match phenotypic latitudinal trends in the wild, suggesting that cogradient variation (Conover and Shultz 1995) may exist for smolt age in Atlantic salmon. In the Connecticut River drainage, juvenile salmon typically smolt after 1 (Farmington River) or 2 years (majority of drainage), whereas in Maine rivers (East Machias, Narraguagus, Sheepscot, and Penobscot), juveniles commonly smolt at age 2+ and age 3+ and only rarely at age 1+ or age 4+ (Baum 1997; USASAC 2003). Similar trends of Atlantic salmon smolt age decreasing with latitude were found in a range of streams in North America (Metcalfe and Thorpe 1990) and between two European populations (Nicieza et al. 1994).

In conclusion, by demonstrating that the degree of stock variation can change throughout the freshwater phase of development in juvenile Atlantic salmon, the results of this study underscore the importance of examining multiple traits at more than one life stage. Had this study only compared growth among stocks for a few months beyond the onset of exogenous feeding or had we only measured size and not hatch timing during the alevin stage, we would have concluded that the five stocks were not different from each other. Additionally, examination over the whole freshwater portion of the life cycle helped further our understanding of the sources of variation at different stages. For example, lack of variation during the spring and summer helped confirm that size differences in autumn were genetically based as opposed to a consequence of inherited maternal environmental effects. When common environment studies conducted on single traits or at short intervals are used to assist with stock differentiation, they should be considered in a broad context covering a large portion of the life cycle.

This study suggests that in addition to influences on stock variation arising from natural selection or inherited maternal environmental effects, artificial selection may be a strong force driving stock differences in intensively managed populations. Stockwell et al. (2003) argue that rapid or "contemporary" evolution should be considered in conservation efforts and that it is of concern for intensively managed and endangered species. In salmon populations undergoing hatchery supplementation, rapid evolution through artificial selection can cause striking genetic differences in a short period of time, which may reduce fitness in the wild and the success of restoration programs (Heath et al. 2003). If artificial selection from hatchery supplementation is driving rapid evolution towards an earlier smolt age in the CT population, the fitness consequences of this change should be evaluated. Two possible opposing effects on survival include (*i*) increasing freshwater survival by shortening the stream portion of the life cycle and (*ii*) reducing marine survival by influencing size at smoltification. Letcher et al. (2002) showed reduced survival in fresh water for CT parr in their second winter. While early marine growth and survival remain poorly understood, a possible consequence of early (age 1+) smoltification is to reach high productivity in the marine environment 1 year sooner. On the other hand, because smolt size increases with smolt age (Okland et al. 1993; Nicieza et al. 1994) and smolt size is positively correlated with adult return rates (Eriksson et al. 1987; Lundqvist et al. 1994), increasing the proportion of age-1+ smolts may reduce survival overall. In either case, unintentional alteration of smolt age in the CT could be influencing population dynamics and smolt production in this stock, and, in turn, the chances for successful restoration.

This study provides evidence that genetically based differences exist among New England Atlantic salmon stocks. Although genetic effects could not be entirely separated from maternal effects for alevin size variation, it is likely that differences in hatch timing and smolt age had a genetic basis. Further studies comparing wild phenotypes and variation of environmental variables among New England rivers would help determine whether the differences we found in these freshwater growth and development traits are a result of adaptations to river-specific environments or a result of artificial hatchery selection.

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Spatial distribution of juvenile Atlantic salmon (*Salmo salar*) in a subarctic river: size-specific changes in a strongly seasonal environment[1]

Aki Mäki-Petäys, Jaakko Erkinaro, Eero Niemelä, Ari Huusko, and Timo Muotka

Abstract: We examined seasonal variation in the spatial distribution and habitat preference of juvenile Atlantic salmon (*Salmo salar*) in a subarctic river characterized by near-zero water temperatures for 7–8 months a year. Size-specific differences in habitat use were pronounced in summer but disappeared at the onset of winter, when the habitats preferred by small (≤6 cm) and larger (7–17 cm) salmon overlapped heavily. Small salmon favoured low-velocity habitats during all seasons, and in summer and autumn they mainly occupied shallow microhabitats along stream margins. In winter and spring, small salmon preferred deeper habitats farther away from the shoreline. Larger salmon favoured deeper habitats in all seasons, but they only occupied slowly flowing areas at low water temperatures. Since all salmon size classes were closely associated with deep and low-velocity habitats in winter and spring, this time of year may represent a size-selective bottleneck for Atlantic salmon populations. Therefore, management schemes aiming to enhance salmonid habitats in boreal streams must rest on the knowledge of season- and size-specific habitat requirements of salmonid species.

Résumé : Nous avons étudié la variation saisonnière de la répartition spatiale et du choix d'habitat chez de jeunes saumons atlantiques (*Salmo salar*) dans une rivière subarctique dont les eaux sont près du point de congélation pendant 7–8 mois par année. Il y a d'importantes différences d'utilisation de l'habitat en fonction de la taille en été qui disparaissent au début de l'hiver; à ce moment, il y a beaucoup de recoupement entre les habitats choisis par les petits saumons (≤6 cm) et les plus grands (7–17 cm). Les petits saumons choisissent des habitats à courant faible en toute saison; à l'été et à l'automne, ils se retrouvent surtout dans les microhabitats peu profonds le long des berges. En hiver et au printemps, les petits saumons choisissent des habitats plus profonds et plus éloignés du bord. Les saumons plus grands choisissent des habitats plus profonds en toute saison et ils n'occupent les milieux à courant faible qu'à température basse. Puisque les saumons de toutes tailles sont fortement associés aux habitats profonds à courant faible en hiver et au printemps, cette période de l'année peut représenter un goulot d'étranglement en fonction de la taille chez les populations du saumon atlantique. Les plans d'aménagement pour améliorer les habitats du saumon dans les cours d'eau nordiques doivent donc se baser sur la connaissance des besoins en habitat des différentes espèces de saumons en fonction de la saison et de la taille.

[Traduit par la Rédaction]

Introduction

Only a small proportion of microhabitats available in a stream reach are suitable for stream-dwelling fish. For instance, Allen (1969) concluded that only 2%–20% of the streambed appeared to have suitable characteristics for the territories of any size class of salmonids. For this reason, many fish enhancement projects aim to increase streambed complexity and thereby the amount of habitat suitable for stream salmonids (e.g., Solazzi et al. 2000). Such attempts to improve salmonid habitat are often based on fish-habitat models constructed for predicting fish population responses to various stream management options (Armstrong et al. 2003).

Assuming that habitat selection bears direct fitness consequences, stream-dwelling salmonids should balance among

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A. Mäki-Petäys,[2] J. Erkinaro, and Eero Niemelä. Finnish Game and Fisheries Research Institute, Oulu Game and Fisheries Research, FIN-90570 Oulu, Finland.
A. Huusko. Finnish Game and Fisheries Research Institute, Kainuu Fisheries Research and Aquaculture, FIN-88300 Paltamo, Finland.
T. Muotka. Finnish Environment Institute, P.O. Box 140, FIN-00251, Helsinki, and Department of Biology, P.O. Box 3000, FIN-90014 University of Oulu, Finland.

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[2]Corresponding author (e-mail: aki.maki-petays@rktl.fi).

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swimming costs, prey capture success, and risk from predators or adverse environmental conditions (Hughes and Dill 1990; Heggenes et al. 1993). Based on the relationship between fitness components and prevailing environmental conditions, one should be able to predict habitat selection and thereby the distribution and abundance of fish (Kramer et al. 1997). However, because both abiotic and biotic factors change over different spatio-temporal scales in all stream environments, it will be a complicated task to predict which particular habitats fish should occupy under varying stream conditions.

The habitat requirements of stream salmonids and their life stages are reported in numerous studies focusing on, for example, habitat and food availability, competition, predation, water temperature, time of day, or discharge (for reviews, see Heggenes et al. 1999; Armstrong et al. 2003). From a management point of view, however, the most important task is to identify the critical habitat factors that limit fish production and can be affected by management. To this end, the ecology of the fish in all relevant life history stages must be properly understood. Otherwise, habitat manipulations may be useless or even harmful in terms of fish production (see Armstrong et al. 2003).

Winter habitat plays a key role in regulating the production of salmonid populations in northern streams (Cunjak 1996; Quinn and Peterson 1996). In general, salmonid fish are reportedly day-active, sit-and-wait predators in summer (Hughes and Dill 1990; Heggenes et al. 1993), whereas at the onset of winter they adopt a shelter-and-move strategy, avoiding the risks of predation and ice damage by being active at night and seeking shelter in the streambed during the day (e.g., Heggenes et al. 1993; Heggenes and Dokk 2001). In contrast to this general pattern, however, Gries et al. (1997) found nocturnal activity in juvenile Atlantic salmon (*Salmo salar*) also in late summer at relatively high water temperatures.

Notwithstanding the improved understanding of winter ecology of stream fish, we still have much to learn about the winter habitat requirements of stream salmonids (Cunjak 1996). For instance, while salmonids are known to undergo marked ontogenetic niche shifts in summer (e.g., Heggenes 1990; Greenberg et al. 1996; Mäki-Petäys et al. 1997), seasonal shifts in size-structured habitat requirements from summer to winter are reported only for brown trout (*Salmo trutta*) (Mäki-Petäys et al. 1997). Because the overwinter survival of juvenile salmonids may be size-dependent (Quinn and Peterson 1996), further research on their habitat selection in winter is urgently needed to facilitate successful management of salmonid fisheries in boreal rivers (see also Cunjak 1996).

We examined seasonal variation in the spatial distribution and habitat preference of juvenile Atlantic salmon in a subarctic river characterized by near-zero water temperatures for 7–8 months a year. First, we developed habitat suitability curves for three size classes of salmon in four seasons (summer to spring). Then, we examined whether the distance from shoreline was different in different seasons and (or) fish size classes. Our study focused on the smallest salmon (≤6 cm standard length), which are often forced to suboptimal habitats by larger and dominant conspecifics (e.g., Vehanen et al. 1999). To test for this pattern in our data, we used a landscape approach, overlaying fish positions onto contours of available habitat, to visualize the habitat use by small salmon in relation to seasonal and spatial variation in habitat conditions. Finally, we studied seasonal variation in the spatial association of the smallest salmon with other salmon size classes present in the study reach.

Materials and methods

Study area

The subarctic River Teno forms the border between northernmost Norway and Finland (70°N, 27°E) and is the most productive and one of the largest salmon rivers in both countries (catchment area 16 386 km^2). Given the size of the river, an annual river catch of 100–200 metric tons (t) of salmon, and high juvenile salmon densities found in the system (Niemelä et al. 1999), River Teno probably supports the largest wild Atlantic salmon population in the world. River Utsjoki is the largest tributary of River Teno on the Finnish side of the drainage basin (1652 km², 66 km in length; Fig. 1), and it also has a considerable run of Atlantic salmon (annual catch 1.5–3 t during the past 10 years; E. Niemelä, unpublished data). The river system is characterized by a large number of lakes; about 93% of the wetted area of River Utsjoki consists of lakes larger than 1 ha. Juvenile salmon is clearly the dominant fish species (>80% in numbers) in the fluvial stretches of River Utsjoki (Niemelä et al. 1999), with only a few, much less abundant cohabiting species, namely European minnow (*Phoxinus phoxinus*), bullhead (*Cottus gobio*), brown trout (*Salmo trutta*), burbot (*Lota lota*), and sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*). Considerable abundances of juvenile salmon have also been detected in the lacustrine habitats of the river (Erkinaro et al. 1998). Water quality in River Utsjoki is good, with pH varying between 6.9 and 7.2, alkalinity between 170 and 290 μequiv.·L^{-1}, conductivity between 3.2 and 4.6 mS·m^{-1}, and total P between 2 and 4 μg·L^{-1}. Water temperature typically reaches a maximum of 13–18 °C in late July – early August. Severe environmental conditions predominate during the winter months, as the water temperature is constantly below 1 °C between late October and mid-May. Ice covers the river for approximately 6 months from November until May.

The study site is located in the lowest part of River Utsjoki, 4 km upstream from the river mouth, in the Mantokoski rapids. This riffle section is 1 km long and 30–40 m wide, rising from the largest lake in the lower part of River Utsjoki, which is Lake Mättajávri (194 ha, maximum depth 60 m). The sampling site was located 100 m below the lake outlet. The site is characterized by open shoreline, relatively fast water velocity, and boulder–cobble substrate (Table 1). Submerged vegetation at the study site was sparse. Despite the harsh conditions during the subarctic winter, small areas in the upper part of the Mantokoski rapids, including our study site, are typically ice-free over the entire winter.

Field protocols

We examined habitat use by juvenile salmon in four seasons: midwinter (February 2002), early spring (April 2002), late summer (August 2002), and late autumn (October 2002). However, because the most pronounced habitat shifts by

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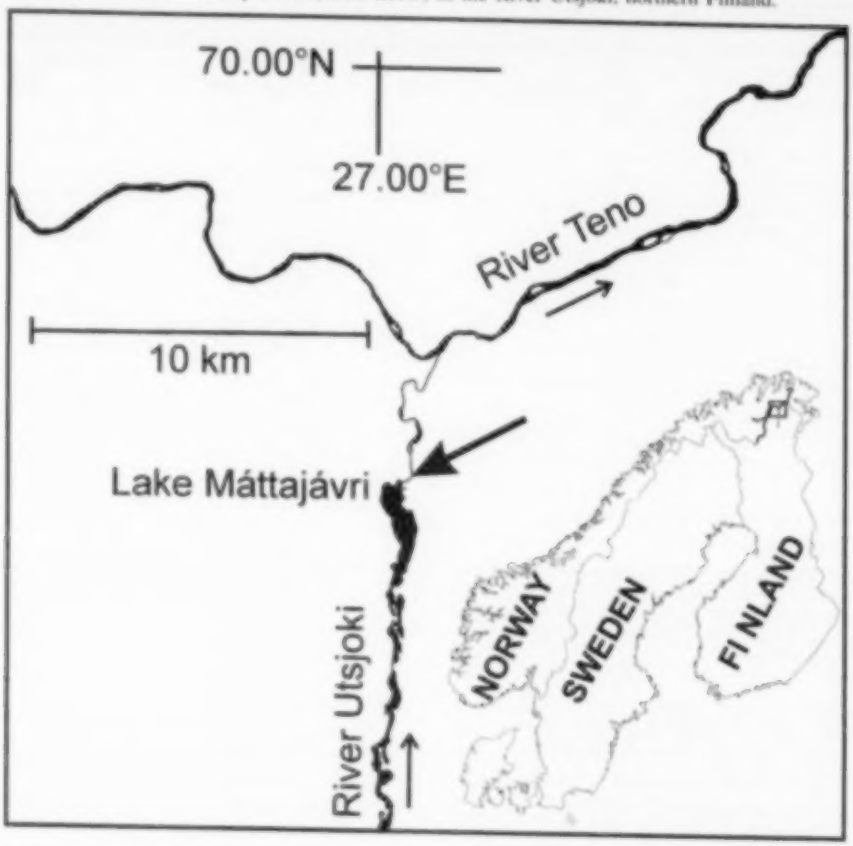
Fig. 1. Location of the study area and the study reach (thick arrow) in the River Utsjoki, northern Finland.



salmonids occur usually at the onset of winter (e.g., Armstrong et al. 2003), we will hereafter follow the more logical order of presentation from summer to spring instead of the original chronology of sampling times.

We fixed a local set of coordinates into a rectangular sampling area, such that the 25-m y axis was directed upstream and the x axis from the left shore to midchannel. The total area sampled and its exact place varied among seasons, because sampling always started from the shoreline, which shifted slightly in different flow and (or) ice conditions. Therefore, the ranges of x coordinates were 1–24 m, 2–19 m, 8–26 m, and 7–26 m in summer, autumn, winter, and spring, respectively. In winter, the total area sampled was also reduced by some ice-covered areas within the sampling site.

We located fish during daylight hours by means of electrofishing, and to eliminate the potential bias caused by interobserver variability, we used the same persons during all field surveys. Although daylight hours in midwinter are short at these latitudes, light intensity during our observation period (1000 to 1400) did not limit fish observations.

According to Heggenes (1990), no method of locating fish (surface observation, diving, electrofishing) works well in all habitat conditions. Efficiency of electrofishing is known to vary among physical habitat types and fish size classes (e.g., Heggenes 1990; Niemelä et al. 2000), which can introduce certain bias to our preference curves. Nevertheless, we chose electrofishing as our method for locating fish, because it has been shown to be the most suitable method for studying habitat use by juvenile salmonids in shallow and fast-flowing streams (Heggenes et al. 1990; mainly <40 cm and >30 cm·s^{-1}). To reduce the potential fright bias caused by this method, we used a point electrofishing procedure suggested by Moyle and Baltz (1985). In addition, we used a 10-cm diameter anode to reduce the positive galvanotaxis induced by DC electroshockers (Copp 1989). A generator supplied a DC current of 900 V at 0.2 A, and the person operating the anode activated it at 0.5-m intervals along cross-sectional transects spaced 1 m apart (y coordinates: 0, 1, 2,..., 25 m) along the sampling area. Two other persons used dipnets to capture stunned fish. The point of the first sighting of a fish was marked with a numbered float anchored to the streambed. The total length of fish was measured to the nearest centimetre, after which they were released back to the stream. A total of 234, 179, 227, and 189 salmon were captured in summer, autumn, winter, and spring, respectively, (Table 1).

Fraser et al. (1995) found that independent of season, juvenile Atlantic salmon become nocturnal as water temperature decreases, moving into streambed shelter by day. In the present study, all the samples were taken by day. This creates the possibility that in cooler seasons, the number of fish

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Table 1. Habitats available for and used by small, medium, and large (4–6 cm, 7–10 cm, and 11–17 cm, respectively) salmon in the Mantokoski rapids, River Utsjoki.

Size class (cm)	Area sampled (m^2)	Water temperature (°C)	Depth (cm)	Mean water velocity ($cm \cdot s^{-1}$)	Dominant substrate (class)	N^a
Summer	538	13.0	39±14.0	80±23.8	6.9±0.8	125
4–6			26±15.8	50±40.2	7.0±1.0	89
7–10			36±14.4	80±45.1	7.5±1.0	81
11–17			39±12.1	96±38.6	7.5±1.0	64
Autumn	400	2.4	34±12.5	53±27.7	7.0±0.8	90
4–6 cm			22±11.0	25±21.8	7.1±0.7	34
7–10 cm			29±14.2	39±29.5	7.1±0.6	78
11–17 cm			35±13.0	48±30.7	7.2±0.6	67
Winter	385	0.5	26±8.5	38±23.4	7.3±0.8	82
4–6			34±7.5	21±13.6	7.0±0.9	21
7–10			31±8.0	30±20.7	6.8±0.9	94
11–17			31±7.7	26±18.2	6.9±0.8	112
Spring	417	1.0	23±10.4	34±23.8	7.0±0.8	98
4–6			33±6.8	23±15.3	6.9±0.5	14
7–10			28±8.5	29±19.8	7.0±0.7	88
11–17			30±7.3	27±19.5	7.1±0.8	87

Note: Substrate is classified according to the Wentworth scale: 1, 0.07–2 mm; 2, 2.1–8 mm; 3, 8.1–16 mm; 4, 16.1–32 mm; 5, 32.1–64 mm; 6, 64.1–128 mm; 7, 128.1–256 mm; 8, 256.1–512 mm; 9, 512.1–1024 mm; 10, bedrock. Means ± standard deviations are shown for depth, mean water velocity, and dominant substrate size.

[a]Number of measurements.

detected might decrease simply because fewer individuals would be available for capture on bed surface. However, this pattern can only obscure the detection of size-specific seasonal changes in habitat use if the behaviour is size-dependent (i.e., only some size classes show this behaviour). Indeed, Valdimarsson et al. (1997) found that smolting juvenile salmon left the shelter by day in spring more frequently than did their smaller resident counterparts. Based on our information on the smolting ages and sizes of salmon in this system (Englund et al. 1999), however, only a few of the largest individuals in this study would be potential smolts the following spring. Therefore, we assumed that different size classes of salmon parr in our study do not show different sheltering behaviours in winter (see also Heggenes and Dokk 2001), and size-dependent seasonal changes in catchability are thus unlikely to affect our results.

Immediately after fish sampling, three habitat variables (depth of water, water velocity, substrate size) and the *x*,*y* coordinates were recorded for each fish position. To quantify habitat availability, we measured the same variables at 1.0-m intervals along six transects (*y* = 0, 5,..., 25 m) at 125, 90, 82, and 98 points in summer, autumn, winter, and spring, respectively (Table 1). Water velocities were measured at 0.6 × depth with a Schiltknecht MiniAir 2 flow meter (Schiltknecht Messtechnik AG, Gossau, Switzerland) fitted with a 20-mm propeller. Dominant substrate was determined visually in 0.8 m × 0.8 m quadrats directly below a fish. Substrate particle size was classified according to a modified Wentworth scale: 1, 0.07–2 mm; 2, 2.1–8 mm; 3, 8.1–16 mm; 4, 16.1–32 mm; 5, 32.1–64 mm ; 6, 64.1–128 mm; 7, 128.1–256 mm; 8, 256.1–512 mm; 9, 512.1–1024 mm; 10, bedrock. After habitat measurements were completed, the shoreline and the boundaries of ice-covered areas, if any, were marked on a detailed map of the sampling area.

Data analysis

We assigned salmon to one of three size classes (4–6, 7–10, 11–17 cm; hereafter small, medium, large, respectively), roughly corresponding to fish ages of 0, 1–2, and 3–5 years, respectively, (Erkinaro and Niemelä 1995). For these salmon size classes, we developed season-specific habitat suitability criteria by constructing suitability curves for each variable using the method described by Baltz (1990). In this procedure, habitat suitabilities, defined as proportional use/proportional availability, were first calculated for each increment of a habitat variable. The resulting indices were then standardized to range from 0.0 (unsuitable) to 1.0 (optimal). Finally, a smoothed suitability curve was fitted to the data using the distance-weighted least squares (DWLS) smoothing option in SYSTAT (Wilkinsson et al. 1992).

To examine the spatial distribution of salmon, we superimposed fish positions on a detailed map of the sampling area separately for each sampling time. These maps were used to measure the distances from each fish position to shoreline. To facilitate among-season comparisons, we related these measurements to the length of the transect sampled (hereafter DS). Thus, for near-shore positions, DS approaches 0.0, whereas DS > 0.5 indicates positions farther than halfway off the shore. A two-way analysis of variance (ANOVA) was conducted on DS to test for potential season × size-class interactions in salmon distribution. If the interaction term was significant, one-way ANOVA followed by pairwise comparisons (Tukey's test) were performed separately for each level of the main effects.

We were specifically interested in whether the spatial distribution of the smallest salmon size class changed among seasons, because in the social hierarchies of stream salmonids, smaller and subordinate fish are often restricted to shallow stream margins or other less suitable habitats (e.g., Elliott

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1994; Vehanen et al. 1999). We therefore superimposed the positions of small salmon onto maps describing the distribution of depth within the study site. These maps were created using the spatial interpolation method of kriging (Surfer for Windows; Golden Software Inc. 1995), which provides estimates for unrecorded locations by minimizing the mean squared prediction error (Cressie 1993). Using these maps, we then measured the nearest-neighbour distances from each small salmon to all other fish, separately for each size class (including other small salmon). The distances were used to calculate Donnelly's (1978) modification of the Clark–Evans (Clark and Evans 1954) index of aggregation (R). The index was defined as (mean distance to nearest neighbour)/(expected distance to nearest neighbour), where expected distance was calculated as $1/(2 \times \text{density}^{0.5})$. A value of $R = 1$ indicates random distribution, whereas spatial pattern is maximally aggregated when R approaches 0.0 and uniform when R obtains values close to its upper limit of 2.15 (Krebs 1989). The deviation of index values from randomness was tested as a normal approximation (Krebs 1989) for each size class of salmon separately for each sampling date. We emphasize that these analyses are not meant to quantify fish territories, but simply to describe seasonal changes in the spatial distribution of salmon size classes in our study area.

Results

Fish densities

When observed across all size classes, total densities of juvenile salmon in summer, autumn, winter, and spring were 43.5, 44.8, 59.0, and 45.3 salmon·100 m^{-2}, respectively. More importantly, however, densities of small salmon decreased from 16.5 fish·100 m^{-2} in summer to 8.5 fish·100 m^{-2} in autumn, whereas concurrent changes for larger salmon were in the opposite direction, increasing from 15.1 to 19.5 fish·100 m^{-2} (medium-sized salmon) and from 11.9 to 16.8 fish·100 m^{-2} (largest salmon). In the previous winter (February to April 2002), densities of small, medium, and large salmon varied between 3.4 and 5.5, 21.1 and 24.4, and 20.9 and 29.1 fish·100 m^{-2}, respectively. However, one should notice that the individuals composing the different size classes in summer and autumn 2002 were either completely (small) or partly (medium and large) different from those in the previous winter. Therefore, an additional electrofishing survey was made to explore the densities of different-sized salmon in winter (March) 2003. The total density was 60.1 fish·100 m^{-2}, and densities of small, medium, and large salmon were 6.9, 27.8, and 25.4 fish·100 m^{-2}, respectively. These figures thus closely paralleled those in February and April 2002.

Ontogenetic and seasonal variation in fish habitat use and preference

Both ontogenetic and seasonal changes in habitat use by salmon were most substantial with respect to water velocity and depth (Fig. 2; Table 1). For small salmon during all seasons, the use of lower velocities than generally available resulted in suitability curves biased towards near-zero velocities, indicating high preference for velocities lower than 20 cm·s^{-1} (Fig. 2*a*). In contrast, the velocities used by medium and large salmon in summer largely paralleled variation in availability. The optimal ranges for velocities were 35–80 cm·s^{-1} for medium and 40–100 cm·s^{-1} for large salmon (Figs. 2*b*–2*c*). However, in low water temperatures (<3 °C) from October to April, the velocity curves for different size classes converged, with medium and large salmon also preferring velocities lower than 20 cm·s^{-1} (Figs. 2*a*–2*c*).

In summer and autumn, large salmon occupied generally deeper stream areas than did smaller salmon (Figs. 2*a*–2*c*). When observed across these two seasons, the ranges of preferred depth were 5–20 cm, 5–35 cm, and 25–60 cm for small, medium, and large salmon, respectively, (Figs. 2*a*–2*c*). However, in winter and spring habitats, the optimal ranges for depth were 30–50 cm for all size classes of salmon. This was mainly because in winter and spring, unlike in summer and autumn, small and medium salmon used stream areas deeper than generally available (Figs. 2*a*–2*c*; see also Figs. 3*a*–3*d*). The depths used by large salmon better reflected the seasonal variation in depth availability, which became biased toward shallow habitats, especially in winter (Table 1).

In summer, pebble–cobble substrates were used selectively by small salmon, whereas medium and large salmon preferred coarser substrates. In other seasons, differences among size classes in substrate preference were negligible. In general, all size classes preferred cobbles or boulders in autumn and slightly finer substrates (large pebbles–cobbles) in winter and spring (Figs. 2*a*–2*c*, Table 1).

Positions of fish in relation to shoreline

Overall, DS did not vary seasonally ($F = 0.92$, df = 3, $p = 0.432$), but DS for small salmon (mean = 0.28) was significantly shorter than that for larger salmon (0.41 for medium and 0.42 for large salmon) (main effect of size class: $F = 8.79$, df = 2, $p < 0.001$, followed by Tukey's tests). More interestingly, season × size-class interactions were also significant ($F = 3.73$, df = 6, $p = 0.001$) (i.e., the effect of size class on DS varied in different seasons (Fig. 4).

In summer, DS differed among the three size classes ($F = 27.02$, df = 2, $p < 0.001$), small salmon being most closely associated with the shoreline and the largest salmon occupying areas farthest from the shore. A similar pattern was also detected in autumn ($F = 11.62$, df = 2, $p < 0.001$), but then only the smallest salmon differed significantly from the other size classes. There were no differences among size classes in winter ($F = 1.26$, df = 2, $p = 0.285$) or in spring ($F = 0.01$, df = 2, $p = 0.989$).

DS varied seasonally for both the smallest ($F = 5.07$, df = 1, $p = 0.002$) and largest ($F = 4.77$, df = 1, $p = 0.003$) salmon, but not for the medium-sized ones ($F = 0.37$, df = 1, $p = 0.776$). Small salmon were closer to the shoreline in summer and autumn than in spring (Fig. 3). In contrast, large salmon occupied areas farther from the shore in summer, but moved closer to the shoreline in winter.

Intra- and inter-cohort spatial associations of small salmon

The mean distances from small salmon to the nearest neighbour in the smallest age group varied between the minimum of 89 cm in summer and the maximum of 249 cm in spring. Distances between the smallest fish and the two larger size groups ranged from 66 to 118 cm in winter and spring

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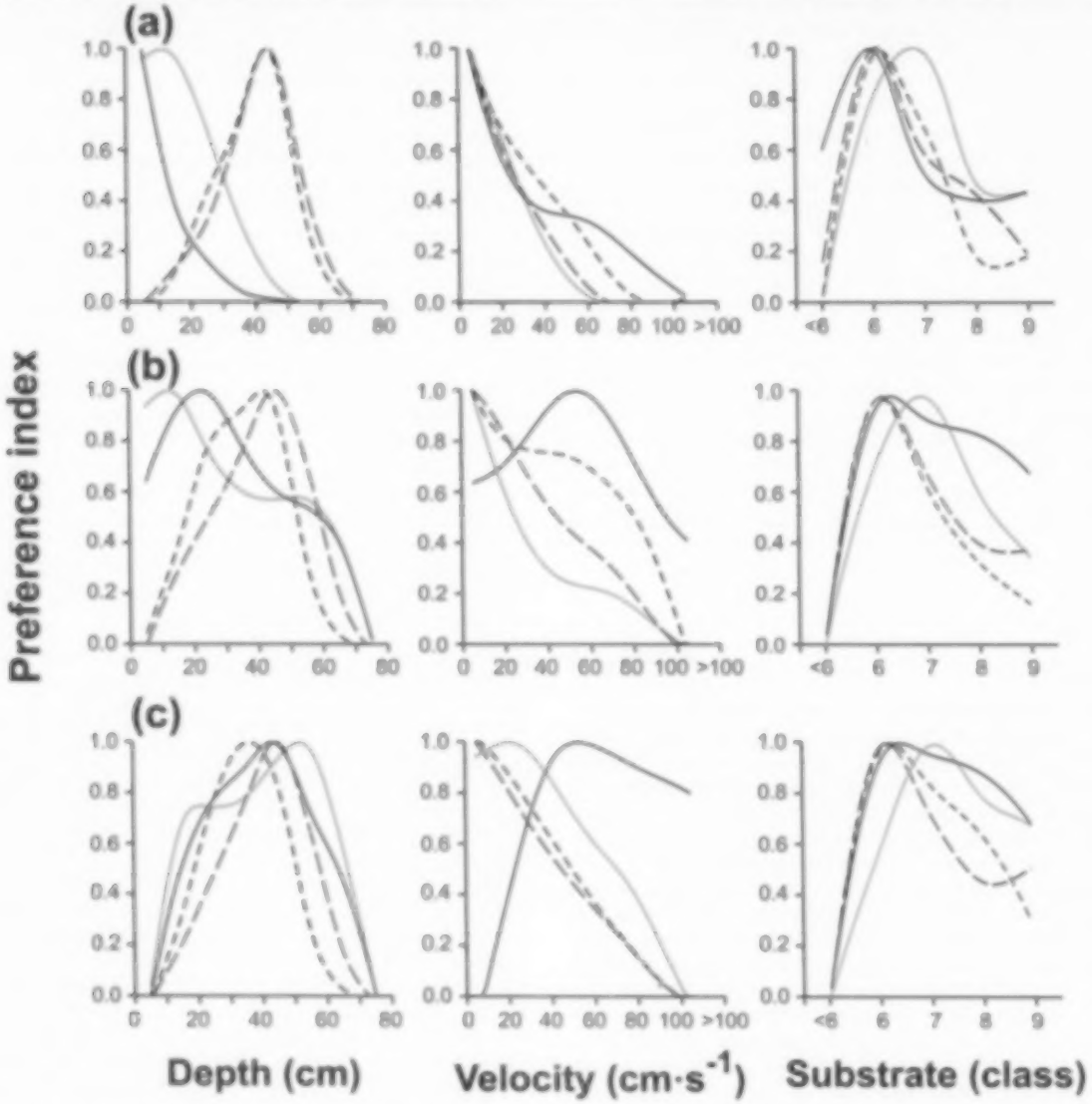
Fig. 2. Suitability curves for depth, mean water velocity, and dominant substrate for juvenile Atlantic salmon (*Salmo salar*) of sizes (*a*) 4–6 cm, (*b*) 7–10 cm, and (*c*) 11–17 cm in four seasons (——, Summer; ·····, Autumn; — —, Winter; – –, Spring).



and from 106 to 174 cm in summer and autumn, respectively, (Table 2).

Small salmon were closely associated with their own size class in summer ($R = 0.69$, $|z| = 5.22$, $p < 0.001$), whereas no deviation from a random distribution was found in other seasons (R values between 0.80 and 0.99, all $p > 0.165$). A parallel seasonal change was detected when the positions of small salmon were related to those of the medium-sized fish (Fig. 5). The distribution pattern between these two size classes was strongly aggregated in summer ($R = 0.83$, $|z| = 2.69$, $p = 0.007$), whereas in other seasons only a tendency toward aggregation was detected (all p between 0.069 and 0.090).

The seasonal distribution of small in relation to large salmon differed distinctly from that found for other size classes (Fig. 5). In summer and autumn, the nearest-neighbour distances from small to large salmon were longer than expected by chance, resulting in a uniform distribution pattern between the size classes ($R = 1.15$, $|z| = 2.08$, $p = 0.038$ for summer and $R = 1.20$, $|z| = 2.99$, $p = 0.003$ for autumn). In contrast, the spatial association was strongly aggregated in winter ($R = 0.69$, $|z| = 5.93$, $p < 0.001$), whereas in spring, the positions of small in relation to large salmon were randomly distributed ($R = 1.03$, $|z| = 0.54$, $p = 0.589$).

Discussion

The bigger fish – deeper habitat relationship frequently documented for stream fishes is mainly related to the risk of predation from aquatic and terrestrial predators (e.g.,

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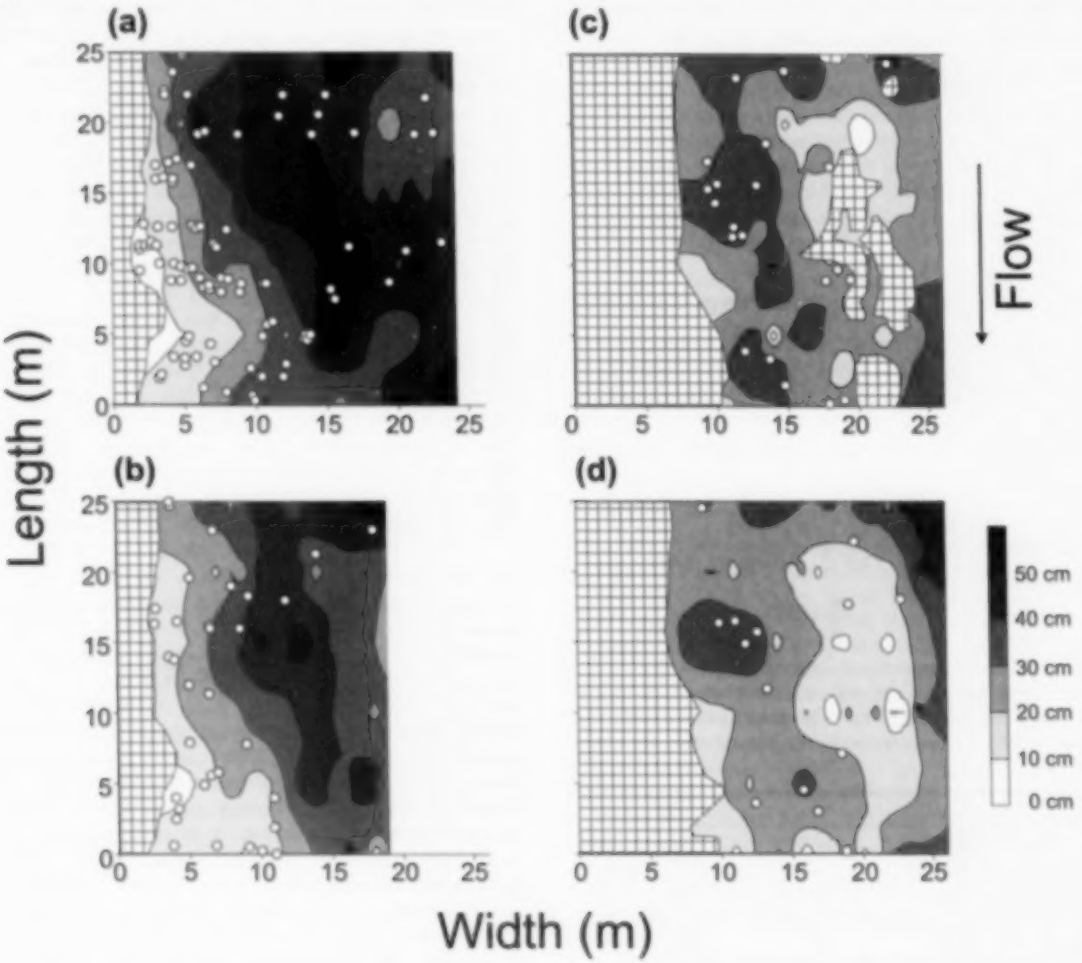
Fig. 3. Overlay maps showing the distributions of small (4–6 cm) salmon (*Salmo salar*) in relation to depth contours within the sampling site in (*a*) summer, (*b*) autumn, (*c*) winter, and (*d*) spring. The depth maps were produced using the spatial interpolation method of kriging.



Schlosser 1987) or to intercohort competition, whereby larger individuals restrict smaller conspecifics to less favourable habitats (e.g., Hughes and Dill 1990). This pattern was also evident in our study, but only for the summertime habitat use by different-sized juvenile Atlantic salmon. Habitat selection was clearly size-structured in summer, with larger salmon preferring deeper and swifter-flowing stream areas with coarser substrates.

At the onset of winter, size-specific habitat use appeared disrupted, as our preference criteria suggested that small salmon were located in deeper habitats further from the shore and larger salmon seemed to select areas with lower velocities than when in their summer habitats. This resulted in relatively similar habitat criteria for all size classes of salmon in winter and spring, whereby deep (30–50 cm), low-velocity (<20 cm·s^{-1}) stream areas with pebble–cobble substrates were preferred by all juvenile salmon, regardless of size. To our knowledge, similar shifts from highly size-structured habitat selection in summer to similar habitat requirements in winter have formerly been reported only for juvenile brown trout (Mäki-Petäys et al. 1997). However, many previous studies conducted either in summer or winter (e.g., Heggenes et al. 1999; Whalen and Parrish 1999; Armstrong et al. 2003) give indirect support to our results. For example, the importance of low-flow refugia to overwintering salmonids is widely recognized, because at low water temperatures fish are less able to hold positions in high-velocity microhabitats (Armstrong et al. 2003). Depth may be less important in winter habitat selection, because salmonids have been reported to use a large variation of depths, from >1-m pools to <20-cm riffles in winter (e.g., Cunjak and Power 1987; Heggenes et al. 1993; Whalen and Parrish 1999). It should be noted, however, that strictly speaking, our preference criteria only hold for fish that remained at our study site. Because the abundance of small salmon decreased about 50% after the summer, it is possible that our curves for small fish at low water temperatures (October, February, April) are biased. Nonetheless, based on extensive research in this part of the river, we know that there is little, if any, better winter habitats for small salmon

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Fig. 4. Relative mean distances to shore from the positions of 4–6 cm (○), 7–10 cm (△), and 11–17 cm (□) salmon (*Salmo salar*) in different seasons. To facilitate among-season comparisons, we related fish-to-shoreline distances to the length of the transects sampled. Error bars indicate 1 standard error of the mean.

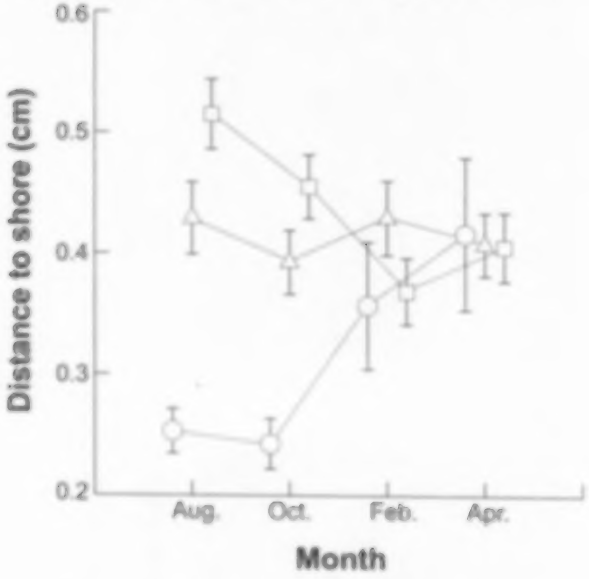


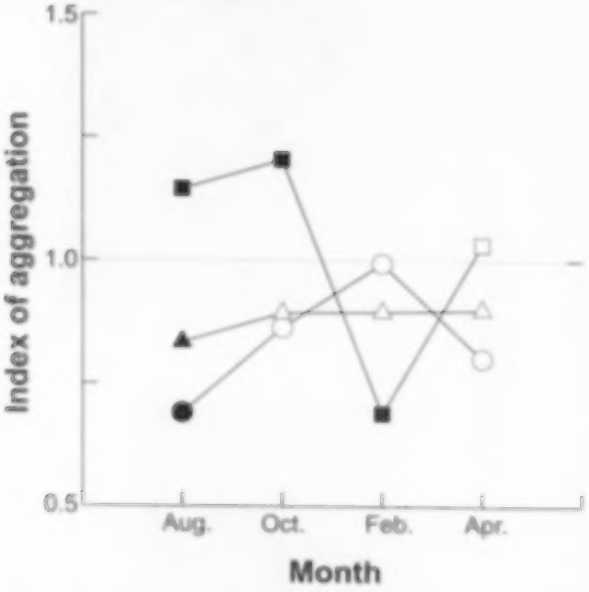
Table 2. Mean distance (cm, range in parentheses) from small salmon to nearest neighbour belonging to small, medium, and large size classes (4–6, 7–10, and 11–17 cm, respectively) in the Mantokoski rapids, River Utsjoki.

	Small	Medium	Large
Summer	89 (6–323)	112 (17–306)	174 (20–460)
Autumn	160 (16–443)	106 (36–272)	154 (32–364)
Winter	237 (44–705)	94 (20–255)	66 (16–187)
Spring	249 (112–801)	102 (18–255)	118 (30–340)

anywhere close to our sampling area within the lowest 4-km stretch of the river below the lake (Erkinaro and Erkinaro 1998; Erkinaro et al. 1998). Some of the fish may enter the lake, but in general, it seems that the apparent survival of 0+ salmon in this area after summer is low — whether this implies emigration, direct mortality, or post-emigration mortality is presently unknown.

Size-related habitat use is generally regarded as a means of avoiding intraspecific overlap in resource use (e.g., Mäki-Petäys et al. 1997). Thus, size-independent habitat selection in winter, if it proves to be more common than previously believed, may have far-reaching effects on wintering salmonid populations. This is especially applicable in severe winter conditions, where ice formation and reduced flow may decrease the amount of habitat suitable for juvenile

Fig. 5. Aggregation indices for small salmon (*Salmo salar*) in relation to the small (4–6 cm; ○), medium (7–10 cm; △), and large (11–17 cm; □) salmon in different seasons. The index values of 0, 1, and 2.15 indicate maximally aggregated, random (horizontal line in figure), and uniform distribution patterns, respectively. Solid symbols show statistically significant ($p < 0.05$) deviation from a random pattern.



salmonids; closely similar habitat selection, or at least overlap in habitat use, by different-sized salmonids may create potential for intensive intraspecific competition (see also Cunjak et al. 1998; Whalen and Parrish 1999). Size-independent habitat selection by juvenile salmonids in winter has also been documented by Jakober et al. (2000), who found a high degree of both intra- and inter-specific overlap in the daytime habitat use by bull trout (*Salvelinus confluentus*) and cutthroat trout (*Oncorhynchus clarki*) in two Rocky Mountain streams. By contrast, Jakober et al. (2000) showed strict habitat partitioning, both among and within species, during winter nights. Based on these findings, competition for suitable winter habitat is more probable during the daylight hours, when salmonids are documented to shelter passively among the substrate (e.g., Heggenes et al. 1999; Heggenes and Dokk 2001).

Intraspecific competition by stream salmonids is generally linked to agonistic behaviour in summer while defending feeding territories. The dominance order and territory size of individuals within social hierarchies are related to prior residence and fish size (e.g., Elliott 1994). The distribution patterns of juvenile salmon in their summer habitats in this study are consistent with these ideas. The close association of small salmon with the shoreline and intercohort habitat segregation may be related to intraspecific competition, whereby only large salmon had access to the most profitable feeding habitats, while small, subordinate individuals were restricted to stream margins.

Contrary to summer associations, small salmon in winter were closely associated with their larger conspecifics. Such

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a pattern has been documented frequently for overwintering salmonids, and it has been typically explained by decreased territorial behaviour at lower water temperatures (Heggenes et al. 1993; Brown 1999; Vehanen and Huusko 2002). For example, Cunjak and Power (1986) concluded that aggregation of trout in winter results from cessation of territorial behaviour. Harwood et al. (2001) suggested, however, that the aggregations result from salmonids defending smaller feeding areas in winter rather than from a total lack of territorial behaviour. Another potential mechanism underlying the shoaling behaviour of salmonids in winter is lowered predation risk. Large aggregations of prey may confuse and inhibit predators, thus reducing the risk of predation for individual fish (Brown 1999). However, we believe this was not the case in our study. Fish species diversity in the study area is extremely low, as not a single specimen of other fish species was captured during our study or on occasional fish samplings outside the study period (J. Erkinaro, unpublished data). Furthermore, a study on diet composition of salmon parr in River Utsjoki revealed no predation on fry by large parr (Erkinaro and Erkinaro 1998). Additionally, our personal observations suggest very little or no terrestrial predators in this part of River Utsjoki. We can therefore safely assume that juvenile salmon in this area are subject to negligible predation threat during winter.

Our observations are consistent with the hypothesis that an insufficient amount of suitable overwintering sites in our study area may have forced small salmon to close association with their larger conspecifics in winter (see also Heggenes et al. 1993; Cunjak 1996; Brown 1999). This may have enhanced competition for space, which is regularly suggested as the primary factor regulating the production of salmonids in winter (Heggenes et al. 1993; Cunjak et al. 1998; Harwood et al. 2001), but the underlying mechanisms are still not well known. Aggressive interactions between conspecifics in natural streams during winter have not been observed for either brown trout (Heggenes et al. 1993) or Atlantic salmon (Whalen and Parrish 1999). However, wintertime aggressions have recently been quantified in laboratory settings for juveniles of rainbow trout (*Oncorhynchus mykiss*) (Gregory and Griffith 1996), brown trout (Vehanen et al. 1999), and Atlantic salmon (Vehanen and Huusko 2002). In a competition experiment simulating wintertime stream conditions, Vehanen et al. (1999) found that age-1 brown trout increased their activity and behaved more aggressively when together with age-0 trout, whereas age-0 trout moved less and were rarely aggressive in the presence of age-1 trout.

Cunjak et al. (1998) suggested that the wintertime aggressions initiated primarily by the largest fry of Atlantic salmon, often resulting in the displacement of smaller and subordinate conspecifics (Cunjak and Randall 1993), might be evidence for wintertime competition. The correlative nature of most field studies gives little insight into the actual mechanisms underlying this behaviour. Accordingly, our results of seasonal changes in habitat selection and distribution of juvenile Atlantic salmon only provide circumstantial evidence for intercohort competition in winter and spring. However, further support is given by size-specific changes of juvenile salmon densities in our study area from summer to spring. During this period, the densities of medium and large-sized salmon increased by 68% and 113%, respectively. At the same time, density of small salmon decreased by 58%. Based on seasonal changes in habitat selection and distribution patterns, we believe that the observed density reduction resulted at least partly from intraspecific competition for suitable refuge space in winter. Therefore, we conclude that in the strongly seasonal environment of boreal streams and rivers, winter may create a size-selective bottleneck for Atlantic salmon populations. We therefore underline that any valid management scheme aiming to enhance stream habitat for salmonids in northern areas needs to rest on the knowledge of season- and size-specific habitat requirements of salmonid species.

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Foraging, growth, and loss rate of young-of-the-year Atlantic salmon (*Salmo salar*) in relation to habitat use in Catamaran Brook, New Brunswick[1]

Isabelle L. Girard, James W.A. Grant, and Stefán Ó. Steingrímsson

Abstract: The ideal despotic distribution predicts that individuals occupying preferred habitats will have higher fitness than those in less preferred habitats, whereas the ideal free distribution predicts that average fitness will be equal in all habitats. To test between these two alternatives, we studied habitat use in relation to foraging, growth, and loss rates of 216 individually tagged young-of-the-year Atlantic salmon (*Salmo salar*). Fish were observed by snorkelling between 2 July and 4 September 1999 in Catamaran Brook, New Brunswick. In a multiple logistic regression, the variables that best discriminated between the habitats used and not used by fish were mean flow velocity and water depth; the fish preferred habitats of intermediate flow velocity (6–48 cm·s^{-1}) and depth (20–39 cm). Fish in preferred habitats experienced higher levels of food abundance and had higher foraging rates but did not differ in body size or growth rate compared with those in less preferred habitats, perhaps because of higher energetic costs. In addition, loss rate did not differ significantly between preferred and less preferred habitats. Our data suggest that salmonid populations at low density may be better described by an ideal free distribution rather than by an ideal despotic one.

Résumé : La distribution idéale despotique prédit que les individus qui occupent les habitats convoités ont une meilleure fitness que ceux qui habitent les habitats moins recherchés, alors que la distribution idéale libre prédit que la fitness moyenne sera la même dans tous les habitats. Afin de choisir entre de ces deux hypothèses, nous avons étudié l'utilisation de l'habitat en fonction de la recherche de la nourriture, de la croissance et des taux de perte chez 216 jeunes saumons atlantiques (*Salmo salar*) de l'année marqués individuellement. La plongée en apnée nous a permis d'observer les poissons entre le 2 juillet et le 4 septembre 1999 à Catamaran Brook, Nouveau-Brunswick. Dans une régression logistique multiple, les variables qui permettent le mieux de discriminer les habitats utilisés et non utilisés par les poissons sont la vitesse moyenne du courant et la profondeur de l'eau; les poissons préfèrent des eaux de courant (6–48 cm·s^{-1}) et de profondeur (20–39 cm) moyens. Par comparaison aux poissons dans les habitats moins recherchés, les poissons dans les habitats préférés ont des densités de nourriture et des taux d'alimentation plus grands, mais ils ne diffèrent pas en taille ou en taux de croissance, probablement à cause de coûts énergétiques plus élevés. De plus, les taux de perte ne varient pas entre les habitats préférés et ceux qui le sont moins. Nos données indiquent que les populations de salmonidés de faible densité peuvent être décrites plus précisément par la distribution idéale libre que la distribution idéale despotique.

[Traduit par la Rédaction]

Introduction

Habitat selection is the non-random use of space that results from the behavioural "decisions" of organisms (Kramer et al. 1997). Because this behaviour defines the realized niche of a species, it has important consequences for the fitness of individuals, the geographical distribution of populations, and the partitioning of resources within communities (Partridge 1978; Kramer et al. 1997).

Habitat selection has been widely studied in stream fishes, partly as a direct response to human impacts on stream ecosystems. Hence, these studies have tended to focus on physi-

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I.L. Girard,[2] J.W.A. Grant,[3] and S.Ó. Steingrímsson.[4] Department of Biology, Concordia University, 7141 Sherbrooke Street West, Montréal, QC H4B 1R6, Canada.

[1]This paper is part of the symposium on The Status of Atlantic Salmon: Populations and Habitats, which took place on 11–14 August 2003 in Québec, Quebec, as part of the 133rd annual meeting of the American Fisheries Society.
[2]Present address: GENIVAR, 5858, chemin de la Côte-des-Neiges, 4e étage, Montréal, QC H3S 1Z1, Canada.
[3]Corresponding author (e-mail: grant@vax2.concordia.ca).
[4]Present address: Holar University College, 551 Saudarkrokur, Iceland.

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cal attributes of habitat to predict the effect of these impacts, such as changes in stream discharge, on the quantity and quality of fish habitat (e.g., Stalnaker and Arnette 1976). Juvenile Atlantic salmon (*Salmo salar*) have attracted considerable attention in this literature because of their economic and cultural value (see Armstrong et al. 2003). In response to the worldwide decline in Atlantic salmon populations (Parrish et al. 1998), conservation and restoration plans now list information about optimal habitat requirements for juveniles as a priority item (Dodson et al. 1998).

Optimal habitats are typically identified as those with the highest population density (see Kramer et al. 1997). Although population density is often correlated with the intrinsic suitability of a habitat (i.e., fitness of individuals when population density approaches zero), the realized suitability of a habitat is density-dependent, because the fitness of individuals often decreases with increasing population density. The ideal free distribution, the most general model of density-dependent habitat selection, predicts that population densities will be directly proportional to habitat productivity such that individuals will have equal fitness across habitats of varying preference and density (Fretwell and Lucas 1970). Hence, no single habitat type is optimal because the best choice for an individual depends on the decisions of others (Kramer et al. 1997). In the ideal despotic distribution, however, aggressive behaviour restricts the entry of individuals into higher quality habitats such that fitness will be higher in preferred habitats with higher population density (Fretwell and Lucas 1970; Kramer et al. 1997). Whether or not fish populations conform to an ideal free distribution versus an ideal despotic distribution has potentially important management implications. In an ideal free distribution, all habitats used by fish will contain high quality individuals and produce recruits to the population, whereas in an ideal despotic distribution, habitat managers will want to focus more narrowly on protecting or augmenting the highest quality habitats occupied by the fish of highest fitness (see Kramer et al. 1997).

By comparing the habitat used with the habitat available in streams, many studies have shown that juvenile Atlantic salmon have distinct habitat "preferences". Of the commonly measured variables, the most important variables influencing habitat selections are typically flow velocity followed by water depth (e.g., deGraaf and Bain 1986; Morantz et al. 1987; Armstrong et al. 2003). Juvenile salmon initially prefer slow flow velocities and shallow water depths but gradually move into faster, deeper water as they grow (Symons and Heland 1978; Rimmer et al. 1984; Morantz et al. 1987).

Quantifying the relationship between population density, or habitat preference, and fitness is crucial for testing between the ideal free and ideal despotic distributions, both of which have been applied to stream salmonids (Pert and Erman 1994; Bult et al. 1999; Armstrong et al. 2002). Because of their conspicuous territorial behaviour (e.g., Keeley and Grant 1995) and limited mobility (e.g., Steingrímsson and Grant 2003), some authors have speculated that salmon populations would conform to an ideal despotic distribution (Kramer et al. 1997; Armstrong et al. 2002). Territorial behaviour, however, does not preclude an ideal free distribution, because territoriality need not have a density-limiting effect (sensu Fretwell and Lucas 1970). Indeed, the ideal free distribution was originally conceived to describe how territorial birds would settle in habitats of varying quality (Fretwell and Lucas 1970).

With two notable exceptions, relatively few studies have measured components of the fitness of fish occupying habitats of differing preference. First, young-of-the-year (YOY) Atlantic salmon preferred habitats that were predicted to provide a high foraging rate (Nislow et al. 1999). Moreover, preferred sites retained a higher proportion of fish over the summer. Second, in an elegant field experiment, juvenile cutthroat trout (*Oncorhynchus clarki*) grew faster in pools, their preferred habitat, than in riffles (Rosenfeld and Boss 2001).

The first goal of our study was to provide a multivariate description of the preferred habitat of YOY Atlantic salmon in the wild. Because of the strong correlation among habitat variables in streams, a multivariate approach is preferable (see Heggenes and Saltveit 1990; Guay et al. 2000) but has rarely been applied to YOY salmon (but see Bremset and Berg 1999). Second, we used foraging rate, growth rate, and loss rate from the study site to estimate components of the fitness of tagged fish occupying habitats of differing preference to test between the alternative predictions of the ideal free and despotic models of habitat distribution.

Materials and methods

Study site and species

We collected data in Catamaran Brook, a third-order tributary of the Little Southwest Miramichi River (46°52′45″N, 66°06′00″W) in central New Brunswick, Canada. Adult Atlantic salmon return to spawn in the river between late September and early November (Cunjak et al. 1993). YOY salmon remain in the stream for 2–3 years before emigrating to sea (Randall 1982; Cunjak et al. 1993). Total watershed area is about 50 km^2, and the stream contains a wide range of habitat types: flats, shallow (<46 cm) and slow flowing (<15 $cm \cdot s^{-1}$); runs, deep (>23 cm) and fast flowing (>15 $cm \cdot s^{-1}$); riffles, shallow (<23 cm) and fast flowing (>15 $cm \cdot s^{-1}$); and pools, deep (>46 cm) and slow flowing (<15 $cm \cdot s^{-1}$) (Cunjak et al. 1993; Gibson et al. 1993). For a more detailed description of the stream and its Atlantic salmon population, see Cunjak et al. (1990, 1993).

Five study sites were chosen approximately 700 m upstream from the mouth of the brook based on two criteria: the combined sites included all four habitat types (i.e., flats, runs, riffles, and pools) and the sites were all located within a 120-m reach in order to detect habitat shifts in individuals that moved between sites (see fig. 1 of Steingrímsson and Grant 2003). On average, the five sites were 16.25 m (range = 15–20 m) in length and 5.88 m (range = 3.30–9.20 m) in width. All sites were repeatedly sampled from 2 July to 4 September 1999 to obtain measurements of the habitat used by and available for the tagged individuals within the sites (Table 1). YOY salmon emerge from the gravel in mid-June and cease growing by mid-September (Randall 1982; Steingrímsson and Grant 1999). For the habitat-use measurements, we subdivided this growing season into early (8–23 July), middle (28 July – 7 August), and late (23–25 August) summer (Table 1).

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Table 1. Schedule of activities during the 1999 field season in Catamaran Brook, New Brunswick.

Round	Dates	Activities	Sites
1	2; 24 July	Measurement of availability of substrate and cover	2–5; 1
	6–7; 9–14; 18–27 July	Tagging and measurement of fork length	2; 5; 1, 3–5
	8; 15; 22–23 July	Habitat-use measurements	2; 5; 1, 3, 4
	23; 24 July	Drift samples; habitat-availability measurements	1–5
2	25–27 July; 4–6 Aug.	Locate tagged fish	1–3; 3–5
	28 July; 6–7 Aug.	Habitat-use measurements	1–3; 3–5
	8 Aug.	Drift samples	1–5
3	10–19 Aug.	Tagging and measurement of fork length	1–5
	20; 21–22 Aug.	Measurements of habitat use and habitat availability	1–5
	22 Aug.	Drift samples	1–5
4	23–25 Aug.	Locate tagged fish; habitat-use measurements	1–5
	26–27 Aug.	Foraging rates of 43 tagged fish	1–5
	29 Aug.	Drift samples	1–5
5	30 Aug. – 2 Sept.	Locate tagged fish; habitat-use measurements	1–5
	3; 4 Sept.	Habitat-availability measurements; drift samples	1–5
	21–30 Sept.	Electrofishing of tagged fish; measurement of fork length	1–5

Habitat availability

The habitat available for YOY salmon was assessed at each site after the habitat-use measurements in early (24 July), middle (21–22 August), and late (3 September) summer, yielding three rounds of habitat availability (Table 1). Within each site, transects were established perpendicular to the flow at 2.5-m intervals. At 1-m intervals along each transect, measurements of flow velocity, water column depth (±0.5 cm, hereafter water depth), substrate size, and the degree of overhead cover were obtained. A portable meter (model 201D; Marsh-McBirney Inc., 4539 Metropolitan Ct., Frederick, MD 21704, USA) was used to measure flow velocity (±0.5 cm·s^{-1}) at the bottom (2 cm above the substrate following deGraaf and Bain 1986), at the mean distance of the fish's snout above the substrate (mean = 3.6 cm) while holding position in the water column at a particular site and time (see Habitat use below), and at 40% of the water depth (hereafter, mean flow velocity). We assessed the degree to which boulders, large woody debris, and water turbulence obscured our ability to see a fish, whether or not one was present, at a particular location. Cover was estimated visually from above the water surface and was categorized as follows: 0, none (fish fully visible); 1, partial (fish partly visible); 2, complete (fish not visible). Substrate size was measured only once, early in the summer (2 July), as it does not vary significantly over the season (deGraaf and Bain 1986; Morantz et al. 1987). At 1-m intervals along the transect, the dominant substrate along a 10-cm line (i.e., 5 cm left and right of each 1-m mark on the measuring tape) was visually estimated and subsequently coded from 1 to 7 using a modified Wentworth scale of particle diameter (mm), similar to the one used by deGraaf and Bain (1986): 1, plant detritus or clay (<0.004); 2, sand or silt (0.004–2); 3, gravel (2–16); 4, pebble (16–64); 5, cobble (64–250); 6, boulder (>250); 7, bedrock.

Tagging individuals and measurements of length

All visible YOY salmon in each site were marked from 6 to 27 July 1999 as part of a larger study of the patterns and correlates of mobility (see Steingrímsson and Grant 2003). A total of 187 fish were captured with dipnets by a diver, who repeatedly snorkelled through each site. Five fish were caught at a time and placed in buckets containing stream water. Each individual was then anaesthetized in a mixture of 3–4 drops of clove oil in 800 mL of water (Keene et al. 1998) and tagged using a 1-cm^3 hypodermic syringe containing fluorescent elastomer paint (Dewey and Zigler 1996).

Individuals were marked using red, green, and orange elastomer at two out of eight possible locations on the fish, creating a distinctive tag for each individual (see Steingrímsson and Grant 2003). Immediately after tagging, the fork length (±0.025 mm) of each individual was measured using callipers. The fish were allowed to recover in a bucket of water for 5–10 min and then were released at their original location of capture. Between 10 and 19 August 1999, 131 tagged individuals and 29 new individuals were retagged or tagged using the same procedure as above. All tagged individuals caught during an electrofishing sweep of all sites on 21–30 September 1999 were measured for fork length (n = 115; 95 of the original 187 fish and 20 of 29 tagged in August).

Habitat use

For each of five rounds of habitat-use measurements, tagged fish were found by repeatedly snorkelling through each of the five sites between 1000 and 1900 (90% between 1300 and 1900), the period of day when YOY are most active (Breau 2003). Each site was sampled an average of 3.6 times per round (range = 1–7) over 1–3 days to ensure a good capture efficiency (see Steingrímsson and Grant 2003). Assuming that 50% of YOY salmon are hiding at any particular time during the day in summer (Breau 2003), on average we should detect 92% of the fish (i.e., $1 - 0.5^{3.6}$). Once a fish was identified, the location where it was first observed that day was marked with a numbered flag embedded in the substrate. The x–y location (±5 cm) of each fish was measured from transects established across each site at 2.5-m intervals. Maps of the x–y data were then created using ArcView GIS 3.2 software (see Steingrímsson and Grant 2003). The distance of the fish's snout above the substrate

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while holding position in the water column was estimated visually.

Once all visible individuals were located, flow velocity (bottom, snout, and mean), water depth, and cover were measured for each numbered flag using the same method described for habitat availability (see above). Substrate size was estimated visually in a 100-cm^2 quadrat around each flag and coded using the same method as above. Sampling all sites took between 5 and 14 days and yielded five rounds of habitat-use measurements for each site (Table 1).

Food abundance

After each of the five rounds of habitat measurements, a drift sample was taken to assess the food available in each site between 1300 and 1830. Benthic samples were not taken as a previous study indicated that most foraging attempts are directed at drifting invertebrates present in the water column and less than 1% of all foraging attempts are directed towards the benthos or the surface of the water column (Keeley and Grant 1995). A 1-m-long drift net with a metal-frame opening of 15.2 cm × 23 cm and a 300-μm mesh size was used to obtain 25 drift samples (i.e., 5 rounds × 5 sites). For each of these five sampling rounds, the drift nets were alternated between a slow-flow station (mean = 4.4 $cm \cdot s^{-1}$, range = 3–9 $cm \cdot s^{-1}$) and a fast-flow station (mean = 22.2 $cm \cdot s^{-1}$, range = 6–59 $cm \cdot s^{-1}$) within each site. To obtain an adequate sample, the drift nets were left longer in slow-flow areas (mean = 99 min) than in fast-flow areas (mean = 61.5 min). Immediately after setting each drift net, the following measurements were taken directly in front of the drift net using the methods described for habitat availability: bottom, snout (i.e., 3.6 cm above the substrate), and mean flow velocity, flow velocity at one-half of drift net height (i.e., 12 cm), water temperature, and water depth. Time of day was recorded at the beginning and end of each drift sample.

All drift samples were preserved in 10% buffered formalin. We processed each sample by removing inedible material such as insect exuviae and plant material. Food items that were considered too big for YOY salmon to eat (Keeley and Grant 1997) were removed from the sample before counting the number of food items. The drift rate at each station and date was expressed as the number of edible organisms captured in a drift net per 20 min. When water depth was less than the depth of the net (23 cm), this rate was prorated to the area of the drift net opening (15.2 cm × 23 cm = 349.6 cm^2).

Foraging rate

To minimize environmental variability while quantifying foraging rate, we concentrated our effort during 2 days (26–27 August 1999) during which no extreme weather events occurred (i.e., rainfall or water temperature). The foraging rate of 43 individuals was measured between 1500 and 1930 and water temperatures between 21.5 and 23.0 °C, the conditions under which YOY salmon are most active (Nislow et al. 1999; Breau 2003). Water clarity was also excellent for observing fish because no major rain event occurred in the previous week. Once a tagged individual was located via snorkelling, the tag of the fish was noted and the fish was allowed to acclimate to the observer's presence (i.e., >1 m downstream of the fish) for 5 min before any measurements were taken (Heggenes and Saltveit 1990). Each individual was then observed for 10 min to count the number of foraging attempts, i.e., rapid movements towards a potential food item.

Statistical analysis

To meet the assumptions of parametric tests, flow velocity, water depth, drift rate, and foraging rate were $\log_{10}$-transformed before analyses. In a few areas of the stream, the flow velocity meter did not detect any flow (i.e., 0.0 $cm \cdot s^{-1}$); these were scored as 0.5 $cm \cdot s^{-1}$ to facilitate the $\log_{10}$ transformation. However, for ease of interpretation, we report the medians or back-transformed means and estimates of variability. When the transformed data did not meet the assumptions of parametric tests, we used non-parametric tests.

Habitat preference was assessed by plotting frequency distributions of the habitat used by salmon versus the habitat available in the stream. Goodness-of-fit tests (i.e., *G* tests; Sokal and Rohlf 1995) were used to test for overall differences between the distributions of use and availability for each variable. Single degrees of freedom (df) χ^2 tests were used to identify significant differences between use and availability for each category of the variable. Habitat preference or avoidance was defined as the use of a habitat category significantly more or less often, respectively, than one would expect based on its availability in the stream.

To use a multiple logistic regression, we transformed our habitat-availability datasets into habitat-not-used datasets by removing all locations that were within the territories of fish. In each of the three sampling periods, all fish in the habitat-use dataset were mapped using ArcView GIS 3.2 software (see Steingrímsson and Grant 2003). For each of these sampling periods, we used Keeley and Grant (1995) to estimate the average territory radius (0.26, 0.35, and 0.40 m, respectively) based on the average fork length of fish (4.47, 5.22, and 5.64 cm, respectively). Any habitat-availability locations that were within these territories were deleted. For each fish in the habitat-use dataset, we then randomly selected one not-used location. We used multiple logistic regressions to determine the key variables that distinguished between used and not-used habitat in early, middle, and late summer (see Guay et al. 2000). The probability of YOY salmon using a habitat was then used as a multivariate measure of habitat preference, which was calculated for the location of each fish and each grid location for each of the early, middle, and late summer samples. We calculated the density of fish in preferred and not-preferred habitats (probability of use >0.50 or <0.50, respectively) by counting the number of fish and the amount of habitat in each category in each sample.

Fork length of the tagged fish (range = 33.1–63.0 mm) increased linearly over the season until it levelled off sharply towards the end of the summer (Girard 2002). We assumed that growth rate had ceased by the time fish were electrofished (i.e., day of year = 264 – 273). A date for the cessation of growth was estimated as the intersection between a linear regression of fork length on date before electrofishing (i.e., day of year < 241) and the mean fork length of fish caught during electrofishing (i.e., fork length = 57.1 mm). The intersection point was on 5 September.

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Hence, we assumed that growth rate was linear over the season and ceased on 5 September (Girard 2002).

Individual growth rate was calculated as (final – initial fork length) × (final – initial day of year of the fork length measurement)$^{-1}$. Because fork length was measured in three separate rounds (Table 1), two measures of growth rate were calculated: early summer (i.e., between rounds 1 and 3) and late summer (i.e., between round 3 and electrofishing).

Results

Of the 216 YOY salmon tagged, 86.6% were relocated sometime throughout the summer. In general, the tagged fish were extremely sedentary, with 96.4% of recaptured fish moving less than 5 m either up- or down-stream from their original tagging location. For a detailed analysis of the movement of these fish, see Steingrímsson and Grant (2003).

Univariate analysis of habitat preference

The three measures of flow velocity (i.e., bottom, snout, and mean) were highly intercorrelated, both for the habitat used by fish (Pearson's correlation, r values > 0.58, n = 737, P values < 0.001) and available in the stream (r values > 0.81, n = 603, P values < 0.001). Also, a multiple logistic regression analysis (see below) showed that the mean flow velocity was the most important of the three in distinguishing between habitat used and not used by YOY salmon. Consequently, we present data only for mean flow velocity, hereafter called flow velocity.

Flow velocity (cm·s^{-1}) available in the stream changed significantly over the summer (repeated-measures analysis of variance, ANOVA, $F_{[2,370]}$ = 66.3, P < 0.001), increasing from early in the summer to mid-summer and then decreasing in late summer (Fig. 1). Flow velocity used by YOY salmon also changed significantly over the five sampling rounds (ANOVA, $F_{[4,264]}$ = 11.4, P < 0.001), in parallel with changes in flow velocity available. Flow velocity used increased from a median of 7.0 in early summer to 12.0 in mid-summer and then decreased to 6.0 in late summer. YOY generally avoided slow flows (<3 cm·s^{-1}) and preferred moderate flows (>6 cm·s^{-1}) (Fig. 1). The distribution of flow velocities used by fish differed significantly from those available in early, middle, and late summer (early, G = 112.6, df = 5, P < 0.001; middle, G = 110.4, df = 5, P < 0.001; late, G = 105.4, df = 5, P < 0.001). Early (Fig. 1*a*) and late (Fig. 1*c*) in the summer, fish significantly preferred flow velocities between 6 and 24 cm·s^{-1} and significantly avoided flow velocities below 1.5 cm·s^{-1} (χ^2 tests, df = 1, P values < 0.005). In mid-summer (Fig. 1*b*), however, YOY significantly preferred flow velocities between 12 and 48 cm·s^{-1} and significantly avoided flow velocities below 3 cm·s^{-1}. YOY salmon were always found less often than expected in flow velocities greater than 48 cm·s^{-1}. These seasonal trends in apparent habitat preference followed seasonal trends in flow velocity in the stream.

Water depth available in the stream changed significantly (ANOVA, $F_{[2,370]}$ = 49.9, P < 0.001) over late summer and showed the same seasonal patterns as flow velocity (Fig. 2). Water depth used by fish in the stream also changed significantly over the five sampling rounds (ANOVA, $F_{[4,264]}$ = 4.91, P < 0.001), increasing from early summer to mid-summer and then decreasing in late summer (Fig. 2). The distribution of water depths used by fish differed significantly from that available in all three time periods (early, G = 101.2, df = 7, P < 0.001; middle, G = 173.6, df = 7, P < 0.001; late, G = 133.5, df = 7, P < 0.001) (Fig. 2). Early (Fig. 2*a*) and late (Fig. 2*c*) in the summer, YOY salmon significantly preferred water depths between 20 and 39 cm and

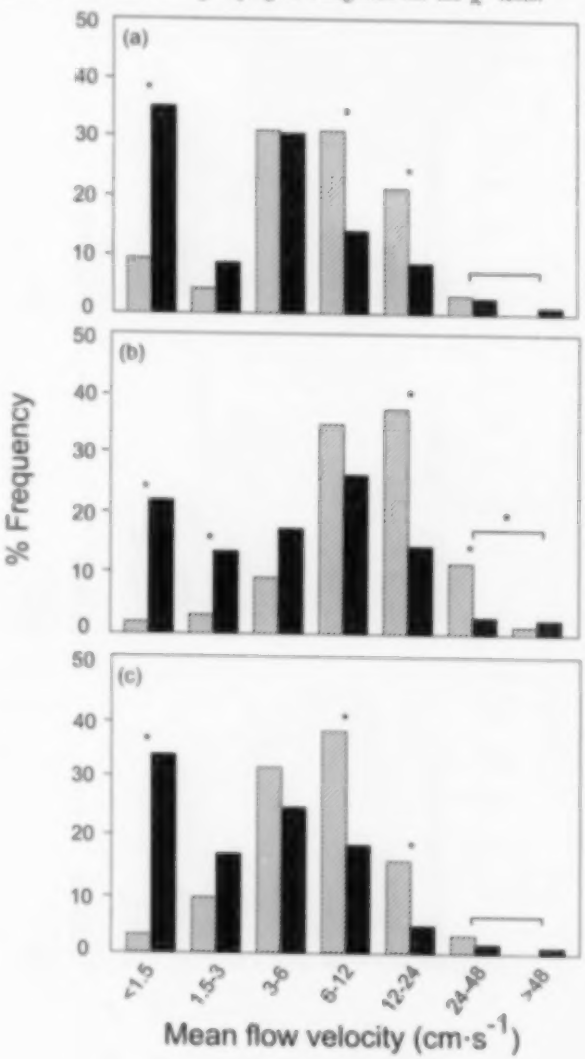

Fig. 1. Frequency distribution of the mean flow velocity of the water column available to (solid bars) and used by (hatched bars) young-of-the-year Atlantic salmon (*Salmo salar*) in (*a*) early (2–28 July; n = 200 and 187 for availability and use, respectively), (*b*) middle (10–22 Aug.; n = 211 and 160 for availability and use, respectively), and (*c*) late summer (30 Aug. – 3 Sept.; n = 192 and 128 for availability and use, respectively) of 1999. Asterisks indicate categories where single-df χ^2 tests yielded significant differences between use and availability. Horizontal lines show the grouping of categories for the χ^2 tests.

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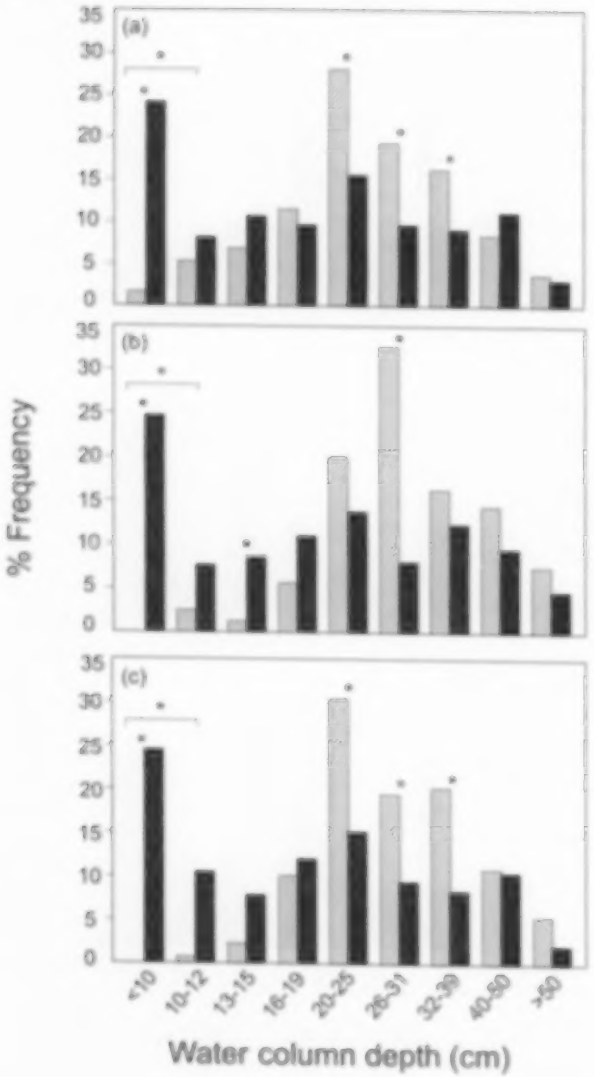
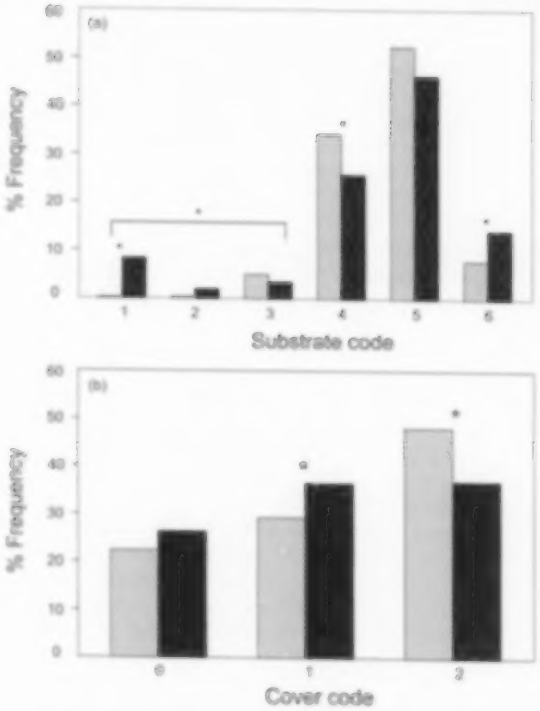
Fig. 2. Frequency distribution of the water depths available to (solid bars) and used by (hatched bars) young-of-the-year Atlantic salmon (*Salmo salar*) in (*a*) early (2–28 July; n = 200 and 187 for availability and use, respectively), (*b*) middle (10–22 Aug.; n = 211 and 160 for availability and use, respectively), and (*c*) late summer (30 Aug. – 3 Sept.; n = 192 and 128 for availability and use, respectively) of 1999. Asterisks indicate categories where single-df χ^2 tests yielded significant differences between use and availability. Horizontal lines show the grouping of categories for the χ^2 tests.



avoided water depths below 12 cm (χ^2 tests, df = 1, P values < 0.005). In mid-summer (Fig. 2*b*), water depths between 26 and 1 cm were significantly preferred, whereas water depths below 15 cm were significantly avoided.

The dominant substrate types available in the stream were pebble and cobble (Fig. 3*a*). The average substrate size used by fish did not change significantly over the summer (median = 4.6, 4.6, and 4.7 in early, mid-, and late summer, respectively; ANOVA, $F_{[4,2864]}$ = 1.41, P = 0.23). Because the availability of substrate and cover was measured only once during the summer, habitat use was combined for all three time periods and then compared with availability. The distribution of substrate used by fish differed significantly from that available in the summer of 1999 (G = 60.3, df = 3, P < 0.001); fish significantly preferred a pebble substrate and significantly avoided boulders and substrates smaller than pebbles (χ^2 tests, df = 1, P values < 0.01) (Fig. 3*a*).

Fig. 3. Frequency distribution of (*a*) substrate sizes (1, plant detritus and particles < 0.004 mm; 2, sand or silt; 3, gravel; 4, pebble; 5, cobble; 6, boulder) and (*b*) degree of overhead cover (0, no cover; 1, partial cover; 2, complete cover) available to (solid bars; n = 205) and used by (hatched bars; n = 475) young-of-the-year Atlantic salmon (*Salmo salar*) in Catamaran Brook in the summer of 1999. Asterisks indicate categories where single-df χ^2 tests yielded significant differences between use and availability. Horizontal lines show the grouping of categories for the χ^2 tests.



The use of cover by fish changed significantly over the summer (G = 14.5, df = 4, P < 0.01, not shown), but fish predominantly used complete cover (47%, 42%, and 59% in the early, mid-, and late summer, respectively). The distribution of cover types used by fish differed significantly from that available in the stream (G = 25.1, df = 2, P < 0.001). YOY salmon significantly preferred complete cover and significantly avoided areas with partial cover (χ^2 tests, df = 1, P values < 0.01) (Fig. 3*b*).

Multivariate analysis of habitat preference

A forward stepwise multiple logistic regression was used to identify the key habitat variables that best differentiated between the habitat used and not used by salmon. A separate

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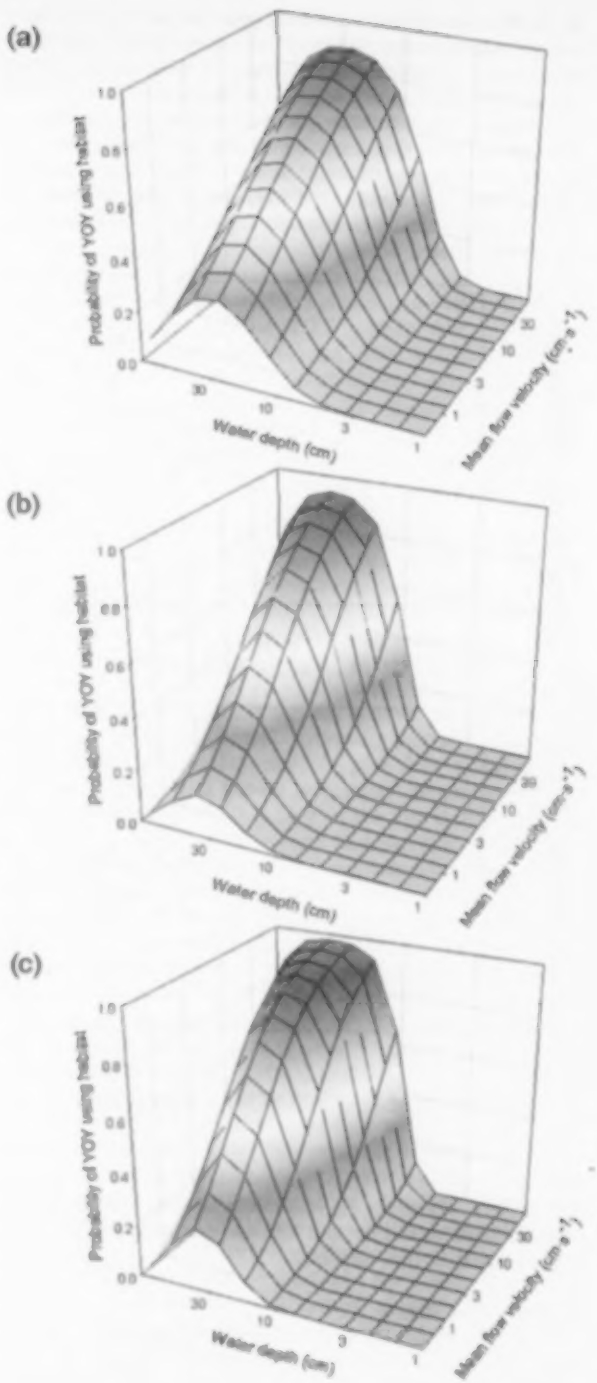
Fig. 4. Multiple logistic regression models relating the probability of young-of-the-year (YOY) Atlantic salmon (*Salmo salar*) using a habitat in relation to flow velocity and water depth in (*a*) early (2–28 July), (*b*) middle (10–22 Aug.), and (*c*) late summer (30 Aug. – 3 Sept.) of 1999. The probability of YOY using a habitat was best described as follows: early, $\log_e(p/1-p) = 1.35 \log_{10}$flow velocity ($m \cdot s^{-1}$) + $18.55\log_{10}$water depth (cm) – $6.39\log_{10}$water depth^2 (cm^2) – 11.13 ($X^2 = 90.69$, $n = 372$, df = 3, $P < 0.001$); mid-summer, $\log_e(p/1-p) = 2.01\log_{10}$flow velocity ($m \cdot s^{-1}$) + $32.15\log_{10}$water depth (cm) – $10.40\log_{10}$water depth^2 (cm^2) – 21.90 ($X^2 = 121.96$, $n = 320$, df = 3, $P < 0.001$); and late summer, $\log_e(p/1-p) = 2.27\log_{10}$flow velocity ($m \cdot s^{-1}$) + $40.40\log_{10}$water depth (cm) – $13.08\log_{10}$water depth^2 (cm^2) – 27.11 ($X^2 = 116.69$, $n = 256$, df = 3, $P < 0.001$).



logistic regression was performed on each time period to explore differences over time. In addition, the statistical significance of all variables raised to a power of 2, as well as all interaction terms, was assessed. Only two key variables contributed significantly to the model for each time period: flow velocity and water depth (logistic regression, early, $X^2 = 90.69$, df = 3, $P < 0.001$, 67.7% correct classification (Fig. 4*a*); middle, $X^2 = 121.96$, df = 3, $P < 0.001$, 75.9% correct classification (Fig. 4*b*); late summer, $X^2 = 116.69$, df = 3, $P < 0.001$, 77.0% correct classification (Fig. 4*c*)). Habitat preference of YOY salmon was consistent throughout the summer; probability of YOY using a habitat increased with flow velocity and increased with water depth until about 30 cm and then decreased (Fig. 4).

The probability of YOY salmon using a habitat was then used as a multivariate measure of habitat preference, which can be assigned to the location of each fish and each grid location in each of the early-, mid-, and late-summer samples. We calculated the density of fish in the preferred and not-preferred habitats, respectively (i.e., probability-of-use scores >0.5 or <0.5, respectively) by counting the number of fish and the amount of habitat in both habitat categories in each of the three samples. The mean density of fish was 8.0 times higher in the preferred (mean = 0.72 m^{-2}, range = 0.69–0.78, $n = 3$) than in the not-preferred (mean = 0.09 m^{-2}, range = 0.06–0.14, $n = 3$) habitats.

Food abundance

The number of organisms captured in a 20-min drift-net sample (mean = 5.7, mean – standard deviation (SD) = 1.35, mean + SD = 23.93) increased with flow velocity (partial correlation, $r = 0.93$, $n = 25$, $P < 0.001$) and decreased with water depth (partial $r = -0.45$, $n = 25$, $P < 0.05$) and day of year (partial $r = -0.60$, $n = 25$, $P < 0.005$). When all three variables were included in a multiple regression, drift rate was best predicted by $\log_{10}$(number of organisms per 20 min) = 1.38 (±standard error 0.093) $\log_{10}$flow velocity ($m \cdot s^{-1}$) – 0.0083 (±0.0020) day of year – 0.94 (±0.401) $\log_{10}$water depth (cm) + 5.48 (±0.819) ($r^2 = 0.96$, $n = 25$, $P < 0.001$). This model was used to predict the number of organisms flowing through the width of a drift net (15.2 cm) for the location of each fish over the summer. The predicted drift rate was prorated to the height of the water column experienced by each fish in each time period. This measure of food availability was then compared with the multivariate habitat preference for fish in early, middle, and late summer.

Over the summer, the predicted drift rate always increased with the probability of YOY using a habitat (Pearson's correlation: early, $r = 0.82$, $n = 186$, $P < 0.001$; middle, $r =$

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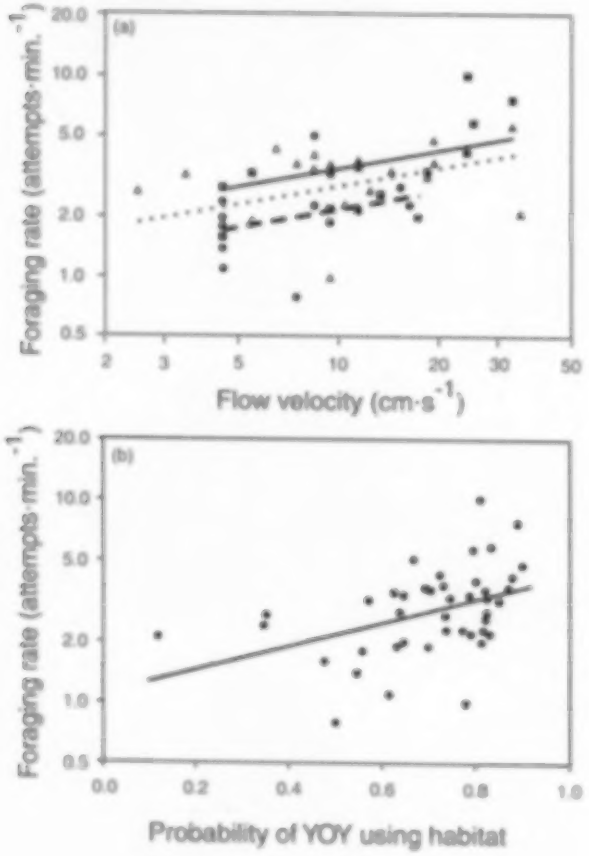
Fig. 5. Relationship between the foraging rate of 43 young-of-the-year (YOY) Atlantic salmon (*Salmo salar*) in late summer (26–27 Aug.) of 1999 and (*a*) mean flow velocity ($m \cdot s^{-1}$) and degree of overhead cover (no cover, ● and broken line, $\log_{10}$foraging rate = $0.302\log_{10}$flow velocity + 0.64; partial cover, ■ and solid line, $\log_{10}$foraging rate = $0.302\log_{10}$flow velocity + 0.84; complete cover, ▲ and dotted line, $\log_{10}$foraging rate = $0.302\log_{10}$flow velocity + 0.76) and (*b*) the probability of YOY using a habitat (average probability between middle and late summer).

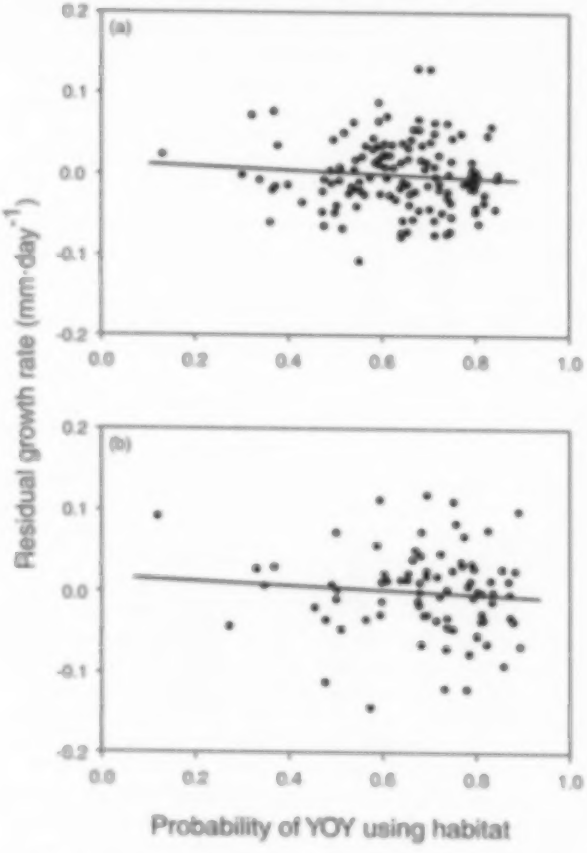


0.85, $n = 155$, $P < 0.001$; late summer, $r = 0.76$, $n = 126$, $P < 0.001$). These strong relationships were not surprising because both drift rate and habitat preference were positively related to flow velocity.

Correlates of fitness

Foraging rate of fish (mean = 2.84 attempts·min^{-1}, mean – SD = 1.71, mean + SD = 4.72) increased with flow velocity (analysis of covariance, ANCOVA, $F_{(1,39)} = 8.93$, $P < 0.005$) and was highest when fish experienced partial cover (ANCOVA, $F_{(2,39)} = 4.00$, $P < 0.05$ (Fig. 5*a*)). Flow velocity and cover combined explained 37.4% of the variation in foraging rate. Foraging rate was not correlated with any other habitat variable (partial r values < 0.28, $n = 43$, P values > 0.05). Foraging rate increased with the probability of YOY using a habitat ($r = 0.43$, $n = 43$, $P < 0.004$; Fig. 5*b*).

Fig. 6. Relationship between residual growth rate and a multivariate measure of habitat preference for (*a*) 132 young-of-the-year (YOY) Atlantic salmon (*Salmo salar*) in early summer (July 6 – 19 Aug.) and (*b*) 81 YOY salmon in late summer (10 Aug. – 30 Sept.) of 1999. Early growth rate was compared with the average of the probability-of-use scores from early and mid-summer, whereas late growth rate was compared with the probability-of-use scores for mid- and late summer.



Growth rate decreased with increasing initial body size for each of the two periods in which growth was assessed (Girard 2002). To control for the effect of initial fork length on growth rate, the residuals from a quadratic relationship (early growth rate (mm·day^{-1}) = 1.880 – 0.0659 fork length (mm) + 0.000640 fork length^2 (mm), $r^2 = 0.330$, $n = 137$, $P < 0.001$; late growth rate (mm·day^{-1}) = 4.050 – 0.139 fork length (mm) + 0.00126 fork length^2 (mm), $r^2 = 0.404$, $n = 107$, $P < 0.001$; see Girard 2002 and fig. 6 of Steingrímsson and Grant 2003) were used as an estimate of early and late growth rate in further analyses. Fish that grew relatively quickly for their length in early summer also tended to grow relatively quickly late in the summer (Pearson's $r = 0.26$, $n = 86$, $P < 0.05$). However, because the correlation was relatively weak, growth rate was analysed separately for early and late summer.

Growth rate in early and late summer was not correlated with the probability of YOY using a habitat (Pearson's r, early, $r = -0.06$, $n = 132$, $P = 0.49$; late, $r = -0.08$, $n = 81$,

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$P = 0.50$ (Fig. 6)). Foraging rate was negatively correlated with late summer growth ($r = -0.48$, $n = 28$, $P < 0.01$; not shown).

To test whether larger fish were found in habitats of higher preference, we compared the size of fish in rounds 1 and 3 and captured via electrofishing with their probability-of-use scores in early, middle, and late summer, respectively. Body size was not significantly related to habitat preference in early (Spearman's $r = -0.063$, $n = 187$, $P = 0.20$), middle (Spearman's $r = 0.097$, $n = 157$, $P = 0.11$), or late (Spearman's $r = -0.128$, $n = 87$, $P = 0.12$) summer.

To test whether loss rate (i.e., mortality and emigration) was related to habitat preference, we noted whether or not the 187 fish tagged in round 1 were captured in the electrofishing survey in late September. Of the 187 fish, 95 were recaptured in the study site at the end of the summer. Whether or not fish were recaptured was not related to their initial habitat preference score in round 1 (logistic regression, $X^2 = 0.03$, df = 1, $P = 0.86$). The percentage lost from the study site was 49% for both preferred (73/148) and not-preferred (19/39) habitats.

Discussion

In the univariate analyses, YOY salmon in Catamaran Brook exhibited distinct habitat preferences for flow velocity, water depth, substrate size, and degree of overhead cover, as documented in many earlier studies (for a review, see Armstrong et al. 2003). In the multiple logistic regressions, however, only flow velocity and water depth significantly discriminated between the habitat used and not used in the stream. Because of the strong correlation among habitat variables in streams, either an experimental approach (Holm et al. 2001) or a multivariate analysis of habitat selection in the wild (see Heggenes and Saltveit 1990; Bremset and Berg 1999; Guay et al. 2000) is required to identify crucial habitat variables for stream fishes.

YOY salmon in our study preferred flow velocities of 6–48 cm·s^{-1} and water depths of 20–39 cm. These results are similar to the preferred flow velocities and depths observed in previous studies of YOY Atlantic salmon: 5–50 cm·s^{-1} and 15–50 cm (deGraaf and Bain 1986); 10–40 cm·s^{-1} and 20–40 cm (Morantz et al. 1987); 20–60 cm·s^{-1} and 15–20 cm (Scruton and Gibson 1993); 8–18 cm·s^{-1} and 10–20 cm (Nislow et al. 1999); and 15–20 cm·s^{-1} (Holm et al. 2001).

Like other studies, flow velocity was the single best variable in our study that discriminated habitat used and not used by fish (deGraaf and Bain 1986; Morantz et al. 1987), presumably because the drift rate of invertebrates increased with increasing flow velocity. Because the energetic costs of capturing prey also increase with increasing flow velocity, whereas prey capture success decreases, a trade-off exists between the benefits and costs of foraging in habitats of varying flow velocity (Hill and Grossman 1993; Nislow et al. 1999). Hence, foraging sites in intermediate flow velocities may be preferred (Nislow et al. 1999) or defended most vigorously (Grant and Noakes 1988).

In our study, YOY Atlantic salmon avoided shallow-water habitats and preferred habitats of intermediate depth, as observed previously in Catamaran Brook (Steingrímsson and Grant 1999) and in other populations (deGraaf and Bain 1986; Morantz et al. 1987). Salmonid fish may avoid shallow water because it restricts the cross-sectional area of stream that can be scanned for food (Hughes and Dill 1990). In addition, they may be more vulnerable to predators in shallow water (Rosenfeld and Boss 2001). YOY salmonids may also avoid or be excluded from deeper water because of competition with larger fish, which occupy deeper and faster water in Catamaran Brook (Keeley and Grant 1995).

Habitat preferences in our study were affected by small temporal changes in habitat availability; the apparent preference for flow velocity paralleled changes in overall flow velocity in the stream. Most YOY salmon were extremely sedentary (Steingrímsson and Grant 2003) and likely tolerate small changes in environmental conditions rather than relocate their home range. This effect was clearly demonstrated in a laboratory experiment where median flow velocity used by YOY salmon increased from 7 to 24 cm·s^{-1} when discharge was increased from 2.6 to 46.8 L·s^{-1} (Holm et al. 2001).

Fish in preferred habitats experienced higher absolute levels of drift and had higher foraging rates but did not differ in body size or growth rate. Growth rate of juvenile salmon is an important component of fitness, because faster-growing fish smolt at a younger age (Hutchings and Jones 1998). However, juvenile salmon trade off the benefits of fast growth for high survival (e.g., Metcalfe et al. 1999), so it was not necessarily surprising that growth rate was not related to habitat preference. However, our loss rate data, which includes mortality rate, suggest that mortality rate also did not vary with habitat preference. Steingrímsson and Grant (2003) estimated that 66% of the loss of fish was due to mortality, based on long-term demographic data. Taken together, these results are more consistent with an ideal free distribution rather than an ideal despotic distribution. The intrinsic benefits of the preferred sites (i.e., higher food availability) were apparently offset by higher population densities and perhaps the higher foraging costs in the faster water (Hill and Grossman 1993; Nislow et al. 1999).

Given the low average density of YOY salmon observed in our study (mean = 0.58 m·s^{-2}, range = 0.08–1.19; Steingrímsson and Grant 2003) and the small size of their territories (Keeley and Grant 1995), we might have expected all fish to settle in the preferred habitats without suffering density-dependent effects. However, the negative effects of density on the growth rate of YOY Atlantic salmon in Catamaran Brook can be detected at densities as low as 0.1 fish·m^{-2} (Imre 2003), densities much lower than one would expect the occurrence of space limitation (sensu Grant and Kramer 1990). Presumably, the density-dependent growth at such low densities occurs primarily via exploitative rather than interference competition (Imre 2003; also see Walters and Juanes 1993). Interestingly, in 1995, the density of YOY salmon in Catamaran Brook declined in a manner consistent with a space-limitation hypothesis (i.e., ideal despotic distribution; Steingrímsson and Grant 1999), when densities were three times higher than observed in our study (mean density in mid-July = 1.97 m^{-2}; Steingrímsson and Grant 1999).

In an ideal free distribution, all habitats occupied by fish will produce individuals of average fitness and, hence, con-

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tribute to the viability of populations. Because juvenile Atlantic salmon tolerate a wide range of conditions (see Nislow et al. 1999; Armstrong et al. 2003), they may provide a relatively broad rearing-habitat niche for habitat managers to target. Whether stream salmonid populations shift between an ideal free and an ideal despotic distribution depending on population density or habitat type (Bult et al. 1999) deserves further study.

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Winter growth and survival of juvenile Atlantic salmon (*Salmo salar*) in experimental raceways[1]

Donna L. Parrish, Ethan J. Hawes, and Kevin G. Whalen

Abstract: We used experimental raceways to determine overwinter mortality of wild-reared immature and mature post-young-of-the-year Atlantic salmon (*Salmo salar*). Secondarily, we investigated the effects of differing treatments (velocity and shelter) on winter growth and survival. Overall survival from November to April was 94%, and survival of immature (98%) and mature (90%) parr, although statistically different, was very similar. Immature parr grew more in length than mature parr, and both immature and mature parr in higher velocity (12 cm·s^{-1}) raceways grew more than those in lower velocity (0.6 cm·s^{-1}) raceways. Stomach contents were twofold greater in parr occupying higher velocity raceways than those in lower velocity raceways. Caloric content of immature and mature parr did not differ in any of five monthly samples. Lowest caloric content occurred in early February and increased between February and March when water temperatures were well below those considered optimal for growth. Although ice cover was present, isolating parr from conditions that occur in natural settings may have helped parr achieve nearly 2.5 times greater survival than parr in the wild. Further, whereas previous studies showed parr select habitats to minimize energetic loss, our results show a distinct advantage for parr to expend energy to feed during winter.

Résumé : Des canaux de nage expérimentaux nous ont servi à déterminer la mortalité en hiver de saumons atlantiques (*Salmo salar*) élevés en nature, tant immatures que matures, mais ayant dépassé le stade de jeunes de l'année. Nous avons aussi étudié les effets de traitements différents (vitesse de courant et refuge) sur la croissance et la survie en hiver. La survie globale de novembre à avril est de 94 % et la survie des tacons immatures (98 %) et celle des tacons matures (90 %), bien que statistiquement différentes, sont très semblables. Les tacons immatures croissent en longueur plus que les tacons matures et les deux types de tacons croissent plus dans des canaux à vitesse de courant élevée (12 cm·s^{-1}) que ceux à vitesse réduite (0,6 cm·s^{-1}). Les contenus stomacaux sont deux fois plus importants chez les tacons vivant dans les canaux à fort courant que ceux dans les canaux à courant réduit. Les contenus calorifiques des tacons immatures et matures ne différaient dans aucun des cinq prélèvements mensuels. Le contenu calorifique le plus faible se retrouve au début de février et augmente entre février et mars à un moment où les températures de l'eau sont bien inférieures aux températures considérées comme optimales pour la croissance. Bien qu'il y ait une couverture de glace, la protection des tacons des conditions du milieu naturel peut les avoir aidés à atteindre une survie presque 2,5 fois plus grande que celle des tacons en nature. De plus, alors que des études antérieures ont montré que les tacons choisissent les habitats afin de minimiser leurs pertes énergétiques, nos résultats montrent qu'il existe un avantage distinct pour les tacons qui dépensent de l'énergie pour s'alimenter en hiver.

[Traduit par la Rédaction]

Introduction

Throughout much of the northern latitudes where riverine systems freeze during winter, many fish species, including Atlantic salmon (*Salmo salar*) juveniles (Cunjak et al. 1998), experience high overwinter mortality. Based on mark–recapture studies, including captures of migrating smolts in streams, winter mortality reaches as much as 60% to 70% in Vermont streams (Whalen et al. 2000). However, these estimates are inherently uncertain, i.e., we never know exactly how many fish were present in the fall, or in the spring, or how many died. Juvenile salmon select specific habitats in winter to reduce energetic costs (Cunjak 1988*a*; Whalen and Parrish 1999*b*), as low water temperatures and dynamic harsh winters can contribute to high mortality (Cunjak et al. 1998). Because of the ephemeral nature of ice

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D.L. Parrish,[2] E.J. Hawes,[3] and K.G. Whalen.[4] Vermont Cooperative Fish and Wildlife Research Unit, US Geological Survey, The Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT 05405, USA.

[1]This paper is part of the symposium on The Status of Atlantic Salmon: Populations and Habitats, which took place on 11–14 August 2003 in Québec, Quebec, as part of the 133rd annual meeting of the American Fisheries Society.
[2]Corresponding author (e-mail: Donna.Parrish@uvm.edu).
[3]Present address: National Marine Fisheries Service, 1 Blackburn Drive, Gloucester, MA 01930, USA.
[4]Present address: US Geological Survey, Biological Resources Discipline, 12201 Sunrise Valley Drive, Reston, VA 20192, USA.

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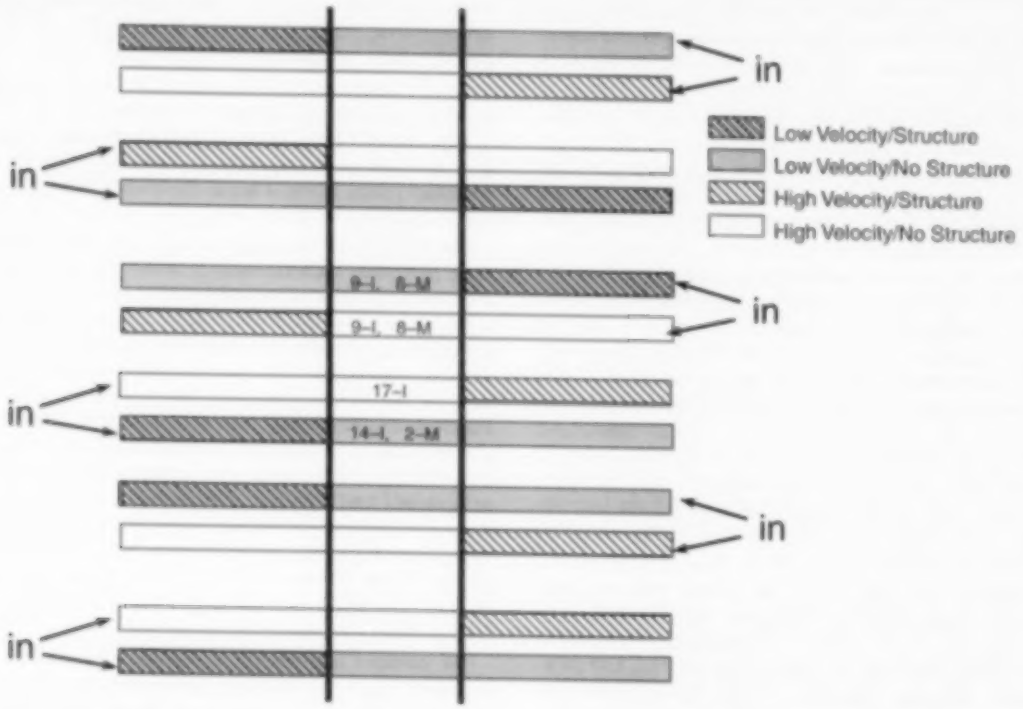
Fig. 1. Locations of the four velocity–structure treatments in hatchery raceways during overwinter experiment. Immature (I, $N = 9$) and mature (M, $N = 8$) parr were placed in each treatment. Additional fish (numbers shown) were placed in four middle sections. Water intake sites are indicated by "in".



formation in streams, Atlantic salmon parr redistribute themselves across habitats as ice forms and melts on a daily basis and temporally affects the character and distribution of high flows (Whalen and Parrish 1999*b*). As optimal or even suboptimal habitats become available and disappear (Whalen et al. 1999), salmon must change behaviors in response to the ensuing increased physiological demands.

Although juvenile Atlantic salmon are known to feed year-round (Cunjak 1988*a*), winter is presumed to be a period of uncertainty for food acquisition because of the dynamic and variable nature of habitat availability caused by ice formation. Two factors that may affect winter survival of parr are their energetic condition entering the winter and their ability to feed during winter to offset accumulated metabolic deficits, such as those associated with fall–winter acclimation (Cunjak 1988*b*). To survive winter, we assume that parr need to maintain a minimal level of condition, as reflected in lipid levels and (or) caloric content (Sutton et al. 2000). For post-young-of-the-year parr, maintaining condition over winter may be critical for smolting and successful spring migration. Currently, it is unknown how environmental conditions during winter influence parr feeding, which affects energetic condition, size and (or) weight maintenance, and ultimately parr survival over the winter period. Generally, the premise is that salmon will opt to be mostly inactive but will need to feed occasionally. The trade-off of eating vs. predation risk indicates that juveniles should be more active at night than during the day (Fraser et al. 1993), despite lower success in foraging at night (Metcalfe et al. 1999).

The maturation of males is of major importance to the condition of Atlantic salmon parr preceding winter (Rowe and Thorpe 1990; Simpson 1992). In Vermont tributaries of the Connecticut River, the percent of males that become mature can exceed 90% (Whalen and Parrish 1999*a*). The energetic investment of becoming fully mature for male parr has been cast as a key component of the life history trade-off of early maturation that could diminish parr condition entering winter and contributes to higher winter mortality of mature parr (Myers et al. 1986). Additionally, within cohorts, mature parr in Connecticut River tributaries are smaller than immature parr in the fall (Whalen and Parrish 1999*a*) and mature parr may adopt behavioral strategies that potentially expose them to higher risk of predation over winter.

We devised an experiment having a primary goal of accurately determining survivorship of Atlantic salmon parr over winter. Secondarily, we addressed (*i*) how differing habitats (velocity and structure) affect growth and survival of immature and mature parr over winter, and (*ii*) how salmon attempt to maintain condition (caloric content) through feeding and activity. We individually marked salmon to determine exactly who grew or not and who died.

Methods

Study site and experimental design

We collected Atlantic salmon parr, which had been stocked as fry, from the Black River in Ludlow, Vermont (43°20′N, 72°36′W), over a 4-day period (14–17 October) in 1997 and used them to establish overwinter treatments in

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hatchery raceways. Parr (N ~ 500, ages 1 and 2, ranging in total length (TL) from 106 to 196 mm) were collected using electrofishing. Fish were transported to the US Fish and Wildlife Service's (USFWS) Pittsford National Fish Hatchery (43°45′N, 73°00′W) in Pittsford, Vermont, on the day of collection and placed into a single raceway. Water for raceways was fed by a gravity-flow multilevel system with most of the water supplied by Furnace Brook, a nearby stream.

The experiment was conducted in 12, 33 m × 2.4 m, uncovered, outdoor raceways (Fig. 1), each separated into three sections by wire mesh screens (1.26-cm^2 mesh, 120 cm high). Each raceway had two 11.5-m-long end sections; thus there were 24 sections in the experiment. We manipulated water depth in the raceways to create high (mean = 12 cm·s^{-1}) and low (mean = 0.6 cm·s^{-1}) velocity conditions. Water depth in the high velocity raceways averaged 26 cm, whereas the low velocity raceways averaged a water depth of 52 cm. We refer to these treatments by their velocities to avoid confusion in denoting both velocity and depth. Water velocity and depth in the raceways also influenced percentage surface ice cover, which was as high as 100% in those with low velocity and remained generally <30% in the high velocity raceways. Ice cover was 100% on low velocity raceways from December to March. No anchor ice was observed in the raceways during the course of the experiment.

Additionally, to provide shelter we added structure consisting of 20 vinyl, opaque, rectangular, open-ended tubes (20.5 cm long × 12.7 cm wide × 7.5 cm high), each placed at a 45° angle to the flow into one of the two 11.5-m raceway sections. This arrangement provided for six replicates of four treatments: (1) high water velocity with structure; (2) high water velocity without structure; (3) low water velocity with structure; and (4) low water velocity without structure. Within each raceway pair, no treatment combinations were alike for sections near the intake (front of raceway) and sections away from the intake (back of raceway). Treatment combinations were also evenly distributed with respect to position (front and back) in the raceway. In January, we lost the data from one low velocity raceway (two treatments: structure and no structure) because a screen partition was breached.

Ice depth to the nearest centimetre, percentage ice cover, water depth to the nearest centimetre, and water velocity measurements were recorded weekly. Although water velocity and depth were determined for all raceways before the experiment, changes in ice cover and ice depth during the study required monitoring weekly. All measurements were taken from five locations: 1, 7.5, 15, 23, and 30 m from the front of each raceway. Water velocity (cm·s^{-1}) was taken with a Swoffer Model 2100 meter (Swoffer Instruments, Inc., Seattle, Wash.) at a water depth of 0.6 m. Two independent readings of percentage ice cover (percentage water surface area covered by ice) were taken for each study section. Water temperature, to the nearest 0.01 °C, was taken every 0.5 h in each raceway with a temperature logger (10 Onset StowAway Tidbits (Onset Computer Corp., Pocasset, Mass.) and two VEMCO Minilogs (VEMCO, Shad Bay, N.S., Canada)). Beginning in mid-November, the average temperature in all treatments was between 0 and 2 °C, but reached a high of 3 °C in early January and never achieved that high again until mid-March. Average temperature differences (maximum – minimum/24-h period) for all treatments was <2 °C until late February when the high velocity treatments began averaging just over 2 °C in daily variation. From mid-March until the end of the experiment, the highest average temperatures achieved were 7 °C, with the highest average daily temperature difference of ~5 °C.

On 9 November, all fish were anesthetized (buffered MS-222, 100 mg·mL^{-1}), sexed, measured (TL) to the nearest 1 mm, weighed to the nearest 0.01 g, and tagged with a 11.5-mm Biomark passive integrated transponder (PIT) tag (Biomark, Inc., Boise, Idaho). Fish were returned to a single raceway for recovery.

On 18 November, eight mature and nine immature fish were placed in each raceway section. The ratio of mature to immature fish placed in each section was the same as the ratio of mature to immature fish collected from the Black River for this study. Densities of fish were initially five to six times greater in the raceways than as determined in the field in late summer, but we do not have parr density estimates available during the winter when usable habitat is highly reduced in streams. There were no significant differences in mean TL (analysis of variance (ANOVA), $p = 0.33$) or weight (ANOVA, $p = 0.20$) of fish across raceway sections. Overall, at the beginning of the experiment, average (±standard deviation (SD)) TL was 146 mm (±17.4) for mature parr and 157 mm (±16.1) for immature parr, and average weight (±SD) was 26.5 g (±11.1) for mature parr and 28.8 g (±9.8) for immature parr.

We counted fish weekly to document mortalities or missing fish. Each month from December through March, between six and 10 immature and mature parr were removed from a cordoned-off central portion of four raceways (Fig. 1) for caloric analysis. Other fish saved for caloric analysis during the experiment included all recently dead fish from the treatments, which were not replaced. Six immature and eight mature fish from each of the two treatments containing structures were used in caloric analysis in April a few days after the experiment. We chose to limit the number of fish used for caloric content so that more fish could be released back into the wild. Therefore, because we knew a few days after the experiment that there were no differences in growth or mortality based on structure, we limited our sample to those from structured treatments.

For caloric workup, fish were removed from raceways and immediately placed on dry ice. Upon return to the lab, fish were sexed, measured, weighed, and placed in a freezer at –15 °C until analyzed. In March, the stomachs of six to 12 parr held in the middle sections from each velocity were removed for weighing. April stomach samples were from the fish as described above for caloric content. Fish selected for caloric and stomach content analysis in each time period were from the spectrum of sizes available. Stomach contents were dried at 60 °C until a constant weight, recorded to the nearest 0.0001 g, was obtained. Fish for caloric analysis were prepared by removing stomach contents and drying bodies to a constant weight (0.001 g) at 60 °C. Individuals were ground to a particle size of 0.5 mm with a Wiley Mill and were bombed according to the Parr instruction manual (Parr 1984). On 10 April, all other fish were removed from experimental sections and were identified, measured, and weighed. Except for those that died or were retained for calo-

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ric content analysis, all fish were released back into the Black River.

Data analysis

PIT tags allowed for tracking survivorship and changes in length and weight of individuals from the beginning to the end of the experiment. We calculated specific growth, which is defined in Ricker (1975) as relative rate of increase (e.g., length is calculated as $L_2 - L_1/L_1$). We tested for differences in specific growth (length and weight) of salmon using a four-way ANOVA, which included the effects of velocity, parr maturity, presence or absence of structure (nested effect), and intake location (near vs. far; see Fig. 1). We used a two-way ANOVA to test for differences in caloric content (wet weight) of mature vs. immature parr across the five seasonal sampling periods. From a small sample of fish, we used a one-way ANOVA to test for differences in amount of stomach contents in March and April across depth–velocity treatments. We calculated the effect size (η^2) for each factor used in the ANOVA models to compare the relative proportion of variance in the respective dependent variable (growth, weight change, and caloric content) attributable to the model-independent variables and model error. We used a Fisher's exact test to evaluate differences in proportional survival between immature and mature parr from November to April.

Results

Overall, fewer immature than mature fish died (Fisher's exact test, $p = 0.003$; Table 1), with mature parr in the high velocity raceways incurring the greatest mortality. However, despite statistical differences, the overall pattern was the extremely high survival of all fish (overall survival = 94%), with 98% of immature and 90% of mature parr surviving from November to April. With so few parr perishing, patterns in the seasonality of mortalities were not evident.

There was suggestive evidence that mortality for the five immature parr that perished during the experiment was size-based. Immature parr that perished were significantly shorter at the beginning of the experiment (*t* test, $p = 0.006$) and weighed significantly less (*t* test, $p = 0.0094$) than immature parr that survived the experiment. For mature parr, there was no significant difference between those that perished and those that survived in either TL (*t* test, $p = 0.59$) or weight (*t* test, $p = 0.76$) at the beginning of the experiment.

Between November and April, immature parr grew in length more (Table 2) and either lost less weight or gained more weight than mature parr (Table 3; Fig. 2*a*). Additionally, both immature and mature parr grew more and either lost less weight or gained more weight in the high velocity raceways than in the low velocity raceways (Fig. 2*a*). On average (±SD), individual mature parr increased 0.0 mm (±2.7) in length in the low velocity raceway and 0.9 mm (±3.4) in length in the high velocity raceway. On average, mature parr lost threefold more weight (mean ± SD = –4.0 g ± 2.4) in the low velocity raceways than in the high velocity raceways (mean ± SD = –1.3 g ± 2.3). Immature parr, on average (±SD), grew 2.7 mm (±2.6) in the high velocity raceways and 0.5 mm (±2.8) in the low velocity raceways. Immature parr, on average (±SD), lost 1.7 g (±1.4) in the low velocity raceways but increased 1.5 g (±2.4) in weight in the high velocity raceways. No differences in either weight (Fig. 2*b*) or length were observed across raceways with or without structure for both velocity treatments.

Table 1. Number of immature and mature Atlantic salmon (*Salmo salar*) parr present at the beginning (November) and end (April) of the experiment at the US Fish and Wildlife Service's Pittsford Fish Hatchery.

	High velocity		Low velocity	
	Immature	Mature	Immature	Mature
November	108	96	90	80
April	104	83	86	74
No. found dead (%)	4 (3.7)	12 (12.5)	2 (2.2)	5 (6.2)
Missing	0	1	1	1

Note: Fish not found dead or alive were classified as missing.

Although both velocity and parr maturity had a significant effect on parr specific growth and weight change over winter, within each respective model, effect size for velocity was greater than that for parr maturity (Tables 2 and 3). These results suggest that over the winter period, environmental factors had a comparatively greater effect on parr specific growth and weight change than parr maturity status.

Although the caloric content of immature parr was on average greater than that of mature parr for all five sample periods throughout the experiment, differences in average caloric content were not significant between immature and mature parr (Table 4; Fig. 3). The only significant seasonal difference in caloric content was observed for immature parr between the second sampling period in January and the third period in February. No other seasonal differences were detected for caloric content for either mature or immature parr. Also, no seasonal vs. maturity interaction was observed for caloric content (Table 4). With the exception of the immature parr caloric content value for the second sampling period in January, the trajectory of caloric content between mature and immature parr was nearly identical (Fig. 3). The lowest caloric content for mature and immature parr occurred in early February, with both groups recovering caloric content between early February and March and through April. The lowest values were in February, with steady increases in calorie averages in March and April.

Because the low velocity raceways were ice-covered for most of the winter, comparisons of amount of food consumed for the two treatments were only available in March and April (Fig. 4). Stomachs of fish in the high velocity raceways weighed twice as much as those in the low velocity raceways (two-sample *t* test, $p = 0.007$ for March and $p = 0.00006$ for April). Additionally, intake position (near vs. far) had a significant effect on weight change over the winter period (Table 2), but not on parr specific growth. Parr residing in raceway sections closer to the intake (flow delivery point) had overall greater weight maintenance than parr residing in raceway sections farther from the intake. Although significant, intake position had a comparatively small effect size on weight change compared with velocity and parr maturity (Table 2).

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Table 2. Summary of statistical output for four-way analysis of variance of effects of parr maturity, intake position, water velocity, and presence/absence of structure on percentage change in total weight of parr between November and April.

Source	df	SS_{effect}	F ratio	Prob > F	Effect size (η^2)
Maturity	1	8985.3	142.7	<0.0001	0.208
Intake position	1	292.7	4.6	0.0317	0.007
Velocity	1	10 910.2	173.2	<0.0001	0.253
Structure [Velocity]*	2	82.4	0.7	0.5203	0.002

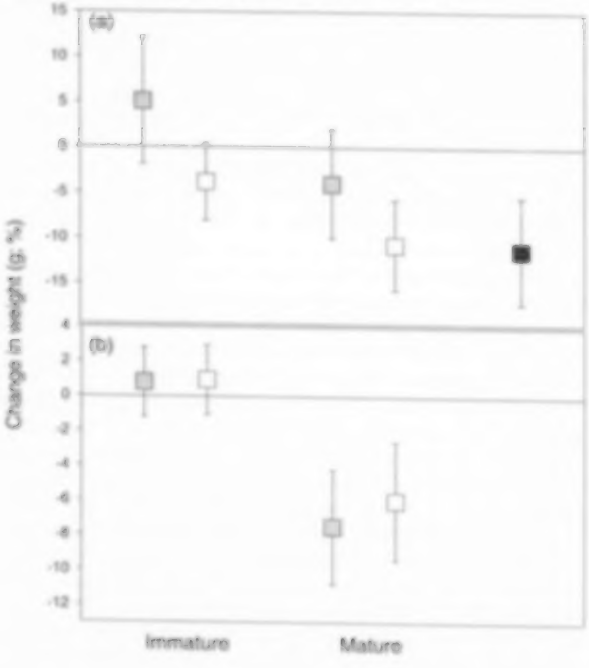
Note: Overall model: $F_{(5,303)} = 64.21$, $p < 0.0001$. SS_{effect}, sum of squares of the effect.
*Structure is nested in velocity.

Table 3. Summary of statistical output for four-way analysis of variance of effects of parr maturity, intake position, water velocity, and presence/absence of structure on percentage change in total length of parr between November and April.

Source	df	SS_{effect}	F ratio	Prob > F	Effect size (η^2)
Maturity	1	60.0	15.2	0.0001	0.037
Intake position	1	2.4	0.6	0.4361	0.001
Velocity	1	105.3	26.7	<0.0001	0.065
Structure [Velocity]*	2	12.5	1.6	0.2074	0.008

Note: Overall model: $F_{(5,307)} = 9.26$, $p < 0.0001$. SS_{effect}, sum of squares of the effect.
*Structure is nested in velocity.

Fig. 2. Change in weight (±standard deviation) of immature and mature Atlantic salmon (*Salmo salar*) parr from (*a*) high (shaded) and low (open) velocity treatments and (*b*) structure (shaded) and no-structure (open) treatments from 20 November to 10 April. Change in weight for mortalities includes immature and mature fish. Mortalities occurred anytime between 20 November and 10 April. Sample sizes are in Table 1.



Discussion

By isolating stream-reared Atlantic salmon parr from the full spectrum of environmental conditions that occur in natural streams during winter, we increased fall-to-spring survival nearly 2.5-fold compared with parr overwintering in fully natural streams. Further, by manipulating water velocity in experimental raceways, we affected parr growth whereby immature and mature parr grew more and either gained weight or lost less weight in higher velocity raceways than parr in lower velocity raceways. Our direct manipulation of environmental conditions during winter and the concomitant positive effects on parr survival, growth, and weight maintenance provide indirect evidence for environmental conditions to be the key determinant of parr recruitment over the winter period.

So why would the great majority of salmon parr survive in hatchery raceways over winter and not do likewise in Vermont streams? Firstly, experimental raceways provided some refuge from predation. Secondly, despite temperatures similar to what the fish would have experienced in the Black River, the raceways provided a much more homogeneous environment than that of a Vermont stream. Parr in our experimental raceways were isolated from the harsher winter conditions that typically occur in Vermont tributaries, including anchor ice, ice damming, high flows, and ice breakup and scour during early spring. Both low and high velocities in the experimental raceways were also in the range of lower velocities that occur in the wild that parr select in the winter (Whalen and Parrish 1999*b*).

Although our results strongly support previous contentions that environmental conditions during winter for stream-reared parr likely contribute significantly to parr winter mortality (Cunjak et al. 1998), we cannot dismiss the likely interaction and (or) role that parr condition may play in winter survival. Parr move over the winter in response to changing ice conditions and occupy and exhibit strong fidelity to sites

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Table 4. Summary of statistical output for two-way analysis of variance of effects of parr maturity and sample period on caloric content of parr (wet weight).

Source	df	SS_{effect}	*F* ratio	Prob > *F*	Effect size (η^2)
Maturity	1	2 265.3	0.153	0.697	0.002
Sample period	4	183 830.6	3.10	0.012	0.155
Sample period × maturity	4	53 372.4	0.900	0.901	0.045

Note: Overall model: $F_{(9,99)} = 2.93$, $p > 0.0047$. SS_{effect}, sum of squares of the effect.

Fig. 3. Caloric content (±standard deviation) of immature (○) and mature (●) Atlantic salmon (*Salmo salar*) parr from December through April held in high velocity hatchery raceways over winter. Sample sizes are given for immature fish above ○ and for mature fish below ●.

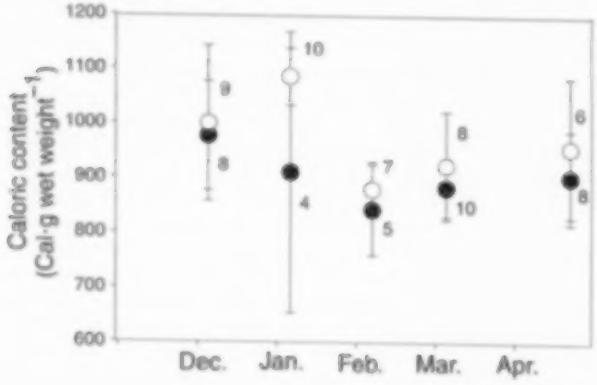
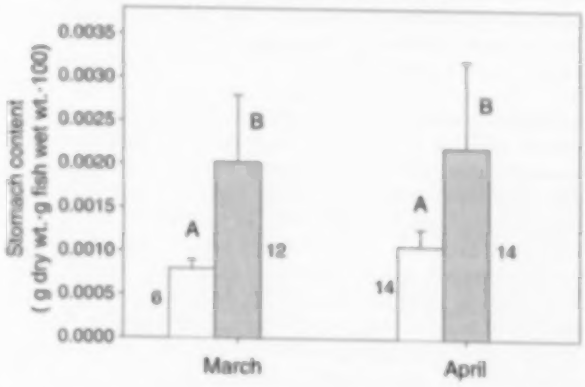


Fig. 4. Mean (±standard deviation) weight-specific dry weight (stomach content dry weight (g) · fish weight^{-1} (g) × 100) of Atlantic salmon (*Salmo salar*) from low (open bars) and high (shaded bars) velocity treatments. Sample sizes are next to bars. Different letters indicate significance at $\alpha = 0.05$.



providing good cover (Whalen et al. 1999). The ability of parr to move and adapt to changing environmental conditions in winter and exploit habitats for feeding in the wild likely could depend strongly on their energetic condition (Simpson 1992). More detailed studies of the interaction between parr energetic state and environmental conditions would provide greater insights into the specific mechanisms causing parr mortality during winter. We suggest that future studies of winter survival include both lake- and estuary-rearing parr, where environmental conditions during winter presumably differ from those found in streams in winter, to provide a more complete picture of winter recruitment dynamics of juvenile Atlantic salmon.

Differences in survival of immature and mature parr, while statistically different, were negligible. Lack of a large difference in winter survival of immature vs. mature parr is consistent with mark–recapture population-level studies in other tributaries of the Connecticut River (Whalen et al. 2000; Letcher et al. 2002). Although immature parr grew more and lost less weight than mature parr from November to April, caloric content of immature and mature parr was very similar before, during, and after winter, with the exception of the January sample period. Thus, our finding of a lack of large-scale difference in survival of immature vs. mature parr is corroborated with a consistent lack of a significant effect of maturation on caloric content of parr over the winter period. Our study confirms that where natural spawning with adult salmon is functionally absent, e.g., Connecticut River tributaries, mature parr do not experience significantly higher winter mortality than immature parr based simply on the energetic vs. growth trade-offs of becoming sexually mature. Our results and those of others working in Connecticut River tributaries (Whalen et al. 2000; Letcher et al. 2002) point to two spawning-related factors as the root causes of higher fall-to-spring mortality for mature parr where it has been observed in the wild (Myers 1984): (*i*) asymmetrical physical interactions among mature parr and adult male salmon that occur during spawning (Hutchings and Myers 1987) and (*ii*) comparatively increased energetic expenditures of mature parr actively engaged in accessing spawning females, or both.

Our manipulation of water velocity in the experimental raceways affected environmental conditions in two ways that may provide some insight into the cost–benefit trade-offs of winter activity and feeding. First, water velocity increased in the low-depth raceways, as did parr feeding. Second, water velocity decreased in the high-depth raceways, which resulted in extensive ice coverage of the raceways for most of the winter. Because the water supply for the experimental raceways was a natural stream, we presume that at least a modicum of aquatic invertebrates were in the water delivery system, which affected food availability directly or provided the invertebrates that we observed to have colonized the raceway surfaces. That salmon parr in the faster flow raceways, which approached natural-conditions parr selected in the wild (Whalen and Parrish 1999*b*), ate more food than those in the extremely slow flows is likely a function of drift-feeding salmon being more likely to consume more prey in higher than lower flows. This conclusion is corroborated by the fact that parr residing in raceway sections closer

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to the flow intake (food delivery area) tended to maintain their weight better than parr residing in raceway sections distant to the intake. The experimental effect of food availability, which we observed serendipitously, provides an explicit link between greater growth and (or) increase in weight or loss of less weight for parr and increased food consumption of parr in the higher velocity raceways.

In contrast, the lower velocity raceways that had extensive surface ice cover during winter presumably would more closely resemble northernmost climates that are subjected to a long period of ice cover (Cunjak et al. 1998). Ice cover provides a stable environment with potentially lower metabolic costs to fish because of the adoption of the torpor mode (Crawshaw 1984). Parr exhibit behaviors to minimize energetic costs in winter that may contribute to higher winter survival, including sheltering in the streambed during the day (Cunjak 1988*b*) and selecting lower water velocities at night (Whalen and Parrish 1999*b*; Whalen et al. 1999). However, at the winter water temperatures of our study, which ranged mostly from 0 to 3 °C, we identified a specific growth and size increase advantage for parr existing in environments that deliver prey, where the costs of feeding by parr must have been offset by the energy gained. Parr move both laterally and longitudinally in streams to avoid space physically excluded by ice and high velocity habitats created by ice formation and to exploit ice as a form of cover when it is available (Whalen et al. 1999). In addition to the maintenance of night activity to avoid ice, particularly in Vermont streams that experience diurnally variable ice formation compared with more northern streams (Cunjak et al. 1998; Whalen et al. 1999), our results suggest that the maintenance of activity during winter for feeding is also adaptive from a metabolic and energy-conservation standpoint. However, some studies using hatchery fish have concluded that parr nocturnal behavior likely results from avoiding diurnal predators (Valdimarsson et al. 1997; Valdimarsson and Metcalfe 1998).

Condition of fish over winter, as determined by weight loss and caloric content, remained quite high. The fish that died had the greatest weight loss regardless of whether or not they were mature. However, we recognize that our mortality results were skewed heavily to mature fish. In Newfoundland, condition and fat content of Atlantic salmon reached the lowest values in April (Sutton et al. 2000); however, no fish were sampled between November and April. Here we show that Atlantic salmon under our experimental conditions experience the lowest caloric values in February. Regardless of the exact timing of the poorest condition, Atlantic salmon increased their fat content rapidly heading into summer (Sutton et al. 2000). Our data on caloric content do not increase as rapidly, but the mean caloric content values increase each month from February to April.

We did not follow the food intake of individual parr over the winter, but the tendency for parr to increase caloric content between early February and March, a period when water temperatures in our experiment and in the wild are well below those considered optimal for growth (10–16 °C; Berg et al. 1990), could indicate that greater feeding over the winter might confer a growth advantage in late winter and early spring compared with parr feeding less. Smolting, future growth and feeding opportunities, and survival during downstream migration have been shown to be size-dependent (Nicieza and Braña 1993). Parr feeding would therefore appear to have an adaptive basis for both forestalling energy loss over the winter and increasing chances of survival, which could provide a greater opportunity for future growth during subsequent smolting and downstream migration.

We suspect that the absence of a significant effect of structure on winter growth and weight gain is because of the low velocities that persisted in the experimental raceways during winter. In the wild, in Vermont tributaries, parr select habitats with lower water velocities (Whalen and Parrish 1999*b*). The higher velocity achieved by manipulating water depth in our experiment was about 12 cm·s^{-1}, which is much closer to the overall average of 18 cm·s^{-1} selected by parr in the wild vs. 0.6 cm·s^{-1} in the low velocity treatments. At higher flows that occur in natural systems in the winter, parr select habitats and seek cover-providing shelter from flows that in some cases locally may exceed 100 cm·s^{-1}. Further, in our experiment, parr were not subjected to predation that may occur in the wild. We surmise that both environmental conditions and potential predation effects did not become significant enough for shelter availability to become a limiting factor for parr survival, growth, or weight maintenance.

A key aspect of the effort to restore Atlantic salmon to the Connecticut River and its tributaries focuses on producing wild-reared smolts from fry stocking. In most Connecticut River tributaries, wild-reared smolts produced from fry stocking spend at least two winters in streams before smolting. After two winters, the numbers of parr becoming smolts are significantly reduced from numbers of fry originally stocked. Before our experiment, it was unknown how parr condition entering winter could affect winter survival and what role environmental conditions have in winter survival of parr. We found that (*i*) isolating parr from conditions that occur in natural settings in winter significantly enhances survival, providing indirect evidence for environmental conditions to be the key determinant of parr recruitment over the winter period, and (*ii*) in addition to selecting habitats to minimize energetic loss, our results show a distinct advantage for parr to expend energy to feed during winter for growth and weight maintenance. A goal of future studies should be to tease apart the effects of winter habitat conditions, salmon metabolic demands, and parr activity vs. the direct effects of predation and the indirect effects of predation risk.

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Energy-related juvenile winter mortality in a northern population of Atlantic salmon (*Salmo salar*)[1]

Anders G. Finstad, Ola Ugedal, Torbjørn Forseth, and Tor F. Næsje

Abstract: By comparing the population frequency distributions for specific somatic energy between samplings using quantile–quantile (QQ) plots, we tested for energy-related mortality of juvenile (2- and 3-year-old) Atlantic salmon (*Salmo salar*) sampled at monthly intervals throughout three consecutive winters in a Norwegian river located at 70°N. Between several of the sampling periods, changes in the distributions of specific energy were observed corresponding to removal of low-energy individuals. By using energetic modelling we demonstrated that metabolic processes or feeding could not be responsible for the shifts in the shape of the energy distributions and that negative-energy-dependent mortality was the most likely explanation for the observations. No changes in mean size of the fish or in the shape of the size distributions were observed between successive sampling periods, indicating that mortality was linked to levels of storage energy rather than to body size per se. Our study indicated a critical body energy level for survival of juvenile salmon at approximately 4400–4800 J·g^{-1}, corresponding to a depletion of storage lipids.

Résumé : En comparant les distributions de fréquence de la population en fonction d'énergies somatiques spécifiques entre les échantillonnages au moyen de diagrammes de type quantile–quantile (QQ), nous avons évalué la mortalité reliée à l'énergie de jeunes (2 et 3 ans d'âge) saumons atlantiques (*Salmo salar*) échantillonnés à intervalles d'un mois au cours de trois hivers consécutifs dans une rivière de Norvège, située à 70°N. Entre plusieurs des périodes d'échantillonnage, il s'est produit des changements de distribution de l'énergie spécifique, qui correspond à un retrait des individus de faible énergie. Au moyen de la modélisation énergétique, nous avons démontré que les processus métaboliques ou l'alimentation ne pouvent être responsables des changements dans la forme des distributions d'énergie et que la mortalité reliée à l'énergie négative est l'explication la plus vraisemblable de ces observations. Nous n'avons pas observé de changements dans la taille moyenne des poissons, ni dans la forme des distributions des tailles entre les périodes successives d'échantillonnage, ce qui indique que la mortalité est reliée au niveau de stockage de l'énergie plutôt qu'à la taille elle-même. Notre étude indique qu'il existe un niveau critique d'énergie corporelle pour la survie des jeunes saumons d'environ 4400–4800 J·g^{-1}, ce qui correspond à l'épuisement des réserves de lipides.

[Traduit par la Rédaction]

Introduction

In animals, available energy through feeding is allocated to maintenance, somatic growth, and reproduction (Calow 1985; Sibly and Calow 1986). Annual patterns in biotic and abiotic environmental factors may lead to seasonal variations in food availability and other environmental adversities. Many animals therefore store energy during periods of surplus feeding in order to mobilise it when food is scarce (e.g., Reznick and Braun 1987; Hutchings et al. 1999). The winter period is often considered to be a survival bottleneck (Cunjak and Therrien 1998; Cunjak et al. 1998), and energy deficiency is one of the suggested main sources of winter mortality for temperate fishes (e.g., Johnson and Evans 1991; Miranda and Hubbard 1994; Cunjak et al. 1998). During summer and autumn, there is a trade-off between energy allocation to storage energy and growth influenced by the allometric scaling of storage capacity, and during winter, the complex allometric relationships of feeding and the allometric scaling of metabolism are suggested as being important for survival (e.g., Schults and Conover 1997; Fullerton et al. 2000; Post and Parkinson 2001).

Empirical evidence for energy-related mortality in natural fish populations is scarce and based on correlations between levels of stored energy and periods with high mortality (Gardiner and Geddes 1980). Indirect evidence has been provided by comparisons of survival of different-sized groups of fish. For several fish species, larger individuals have been shown to have a higher probability of winter survival than smaller, both in experimental studies with simulated winter conditions (Oliver et al. 1979; Post and Evans 1989; Johnson and Evans 1991) and in field studies of natural populations (Post and Evans 1989; Miranda and Hubbard 1994). These

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Anders G. Finstad,[2] Ola Ugedal, Torbjørn Forseth, and Tor F. Næsje. Norwegian Institute for Nature Research, Tungasletta 2, NO-7485 Trondheim, Norway.

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[2]Corresponding author (e-mail: anders.finstad@nina.no).

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observations have been linked to energy-selective mortality through the mass-dependent nature of energetic processes, particularly the increasing depletion rates of energy stores with decreasing size as a result of the allometric scaling of metabolism.

Here, we tested for energy-related mortality in a population of juvenile Atlantic salmon (*Salmo salar*) sampled at monthly intervals throughout three consecutive winters in a Norwegian river located at 70°N. This was done by comparing the population frequency distributions for specific somatic energy between sampling periods. Our main prediction was that selective mortality of low-energy individuals would shift the shape of the distribution. However, similar changes in energy distributions may appear if individuals with low energy status loose disproportionately less energy or have a higher energy intake (e.g., Metcalfe and Thorpe 1992). To test this alternative hypothesis, we employed energetic modelling using population-specific parameters of metabolism and energy-state-dependent food consumption. Finally, we investigate if observed energy-related mortality could be associated with specific levels of total energy and storage lipids.

Material and methods

Study site

The River Alta is situated in northern Norway at 70°N, 23°E (Fig. 1). The catchment area is 7400 km^2, and mean annual water discharge at the outlet is 75 $m^3 \cdot s^{-1}$. The river is regulated for hydropower production with a water reservoir 2.5 km above the end of the salmon-producing area. The power station is located close to the dam, and the outlet from the power station is at the top of the salmon-producing section. Water discharge during the winter period is normally about 31 $m^3 \cdot s^{-1}$ (Fig. 2*b*). Although most of the river is ice-covered during wintertime, salmon parr could be collected because a river stretch below the power station outlet is partly ice-free. In the studied winter periods, mean water temperature was 0.4 °C during January to April, increasing to 1.4 °C during May (Fig. 2*a*). Atlantic salmon is the dominant fish species in the river and can migrate 44 km upstream from the river mouth. The average smolt age is 3.75 years and the frequency of mature parr is low (2%; Heggberget 1987). Twelve other fish species were also found in the river, but they constituted only 2% of the total catch by electrofishing (Heggberget 1987).

Sampling and treatment of material

Atlantic salmon parr were collected by electrofishing in the upper accessible stretches for salmon in the River Alta (Fig. 1) at about 30-day intervals from February to May 2000, January to May 2001, and January to May 2002 (Table 1). The fish were mainly collected from one river section with an area of about 400 m^2. To keep disturbance of fish and area to a minimum, the section was fished only once on each sampling occasion. When necessary, supplementary fish were collected from an adjacent river section. The fish were weighed (±0.01 g) and lengths were measured (total length ± 0.5 mm). Stomach contents and otoliths were removed and the fish were stored at –80 °C until further analyses. Only immature parr of the most numerous age class in the samples, 2-year-olds, as well as the lower size mode of 3-year-old juveniles (<13.0 g), were analysed in the present study. This maximised the number of fish for analyses, as well as maintained a homogenous group, as both 2-year-olds and the lower mode of 3-year-olds are fish that will not smolt the following spring and are thus likely to be in a similar physiological state.

The specific energy ($J \cdot g^{-1}$) of individual fish was estimated from a regression between the dry- to fresh-mass relation (dry-mass percentage) and specific energy (Hartman and Brandt 1995). The dry-mass percentage to specific energy relationship was determined from the proximate composition of lipid and protein in a subsample of fish from January (N = 15), March (N = 15), and May (N = 39) 2001. The mass of the fish in this subsample covered the mass span of the rest of the samples (Table 1). The use of dry mass to energy relations has been advocated as appropriate for predicting both seasonal and ontogenetic changes in energy content of fish (Hartman and Brandt 1995). Furthermore, reanalyses of data presented in Finstad et al. (2003) did not show any significant year effect on the specific energy to dry-mass percentage relationship in Arctic char (*Salvelinus alpinus*), a closely related salmonid. The relationship determined from the 2001 samples was accordingly used to predict energy content in fish from all sampling years. To determine water content of the fish, the carcass, including intestines with fat deposits, was dried in a drying cabinet (70 °C) until a stable dry-mass value was obtained. The individual fish was homogenised, and preweighted subsamples of the homogenate were analysed separately for lipids, water content, and ash content.

Total lipid content was estimated by extraction, using chloroform ($CHCl_3$), methanol (CH_3OH), and distilled water (H_2O) at a ratio of 2:2:1.8 in accordance with the method of Blight and Dyer (1959). To determine triglyceride content, Iastroscan thin-layer chromatography – flame ionisation detector system (TLC–FID) was used for lipid separation. Chromatorods SIII (Iastron Laboratories, Tokyo, Japan) were scanned twice through the Iastroscan FID immediately before sample application to remove impurities. Chloroform solutions (1 µL of a concentration 20 $\mu g \mu L^{-1}$) of the lipid extract were spotted on the Chromarods SIII by the use of a single spotting action and a 10 µL chromatographic syringe. The rods were placed in a development tank. Two different solvent systems were used: hexane – diethyl ether – formic acid (85:15:0.04, by volume) for separating neutral lipids, and chloroform–methanol–water (75:35:3.5, by volume) for separating the polar lipids. The peaks were identified by comparison with known standards (Nu-Chek Prep., Minneapolis, Minnesota, USA).

Ash weight was determined by controlled combustion of a dried subsample of the homogenate at 550 °C. Protein was estimated as the mass proportion of the sample remaining after subtracting the mass proportions of water, lipid, and ash.

Lipid was assigned a caloric value of 39 000 $J \cdot g^{-1}$ and protein a value of 24 000 $J \cdot g^{-1}$ (Jobling 1995). Carbohydrates are a minor body component of teleosts (0.1–0.5% on wet-mass basis) (Craig 1977; Jonsson and Jonsson 1997),

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Fig. 1. Accessible stretches for Atlantic salmon (*Salmo salar*) in the River Alta (70°N, 23°E) in northern Norway. The present study was conducted in the upper parts (study area).

and this component was omitted from the analyses. In the following, energy always refers to mass-specific energy ($J \cdot g^{-1}$) if not otherwise stated.

Detecting changes in energy distributions

During winter, storage energy of juvenile salmonids is usually depleted. Hence it is expected that the mode of the population energy distribution is reduced as winter proceeds. Here we test for depletion of storage energy by investigating differences in mean values of storage energy using analysis of covariance (ANCOVA) with size as covariate and sampling data as factor. If individuals with lower levels of storage energy have higher mortality rates than individuals with high levels, then the shape of the energy distribution will also change. To identify energy-dependent mortality, we therefore test for changes in the shape of the energy distribution. This is done using empirical quantile–quantile (QQ) plots (Sokal and Rohlf 1995) adopting the methodology of

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Fig. 2. (*a*) Temperature (°C) and (*b*) water discharge ($m^3 \cdot s^{-1}$) at the study area for the winters of 2000 (solid lines), 2001 (dotted lines), and 2002 (broken lines).

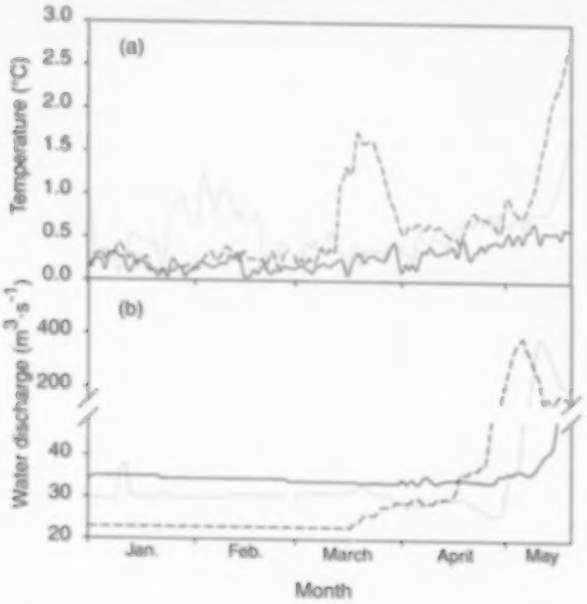
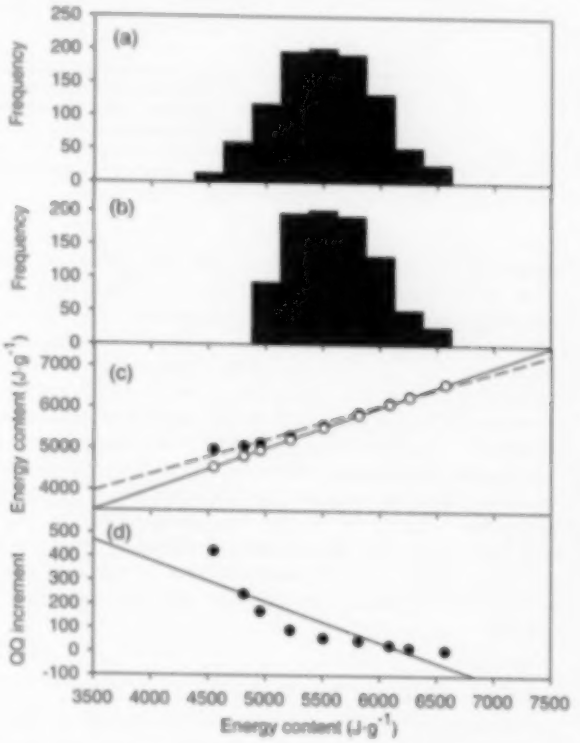


Table 1. Sampling dates of Atlantic salmon (*Salmo salar*) parr in the River Alta, sample sizes (*N*), mean size (fresh mass) with range, and the percent of samples consisting of 2-year-olds.

Sampling date	*N*	Fresh mass (range)	2-year-olds (%)
7 February 2000	35	5.6 (2.4–12.8)	80
6 March 2000	48	5.8 (2.9–12.6)	75
4 April 2000	65	5.6 (2.3–12.9)	78
18 May 2000	13	6.1 (3.1–11.4)	77
23 January 2001	59	6.5 (2.4–12.9)	69
20 February 2001	42	5.9 (2.8–12.5)	74
20 March 2001	68	5.9 (1.7–12.2)	71
18 April 2001	38	5.8 (2.9–12.5)	74
24 May 2001	68	5.8 (2.2–13.0)	72
23 January 2002	42	7.1 (3.1–12.8)	60
20 February 2002	59	6.4 (3.0–12.4)	76
19 March 2002	69	6.2 (2.5–13.0)	72
9 April 2002	47	6.7 (2.2–12.3)	66
23 May 2002	65	6.1 (2.3–12.9)	69

Post and Evans (1989). For two distributions with equal shape, the 5, 10, 25, 50, 75, 90, and 95% quantiles are evenly distributed and will appear on a straight line with slope equal to one when plotted against each other (Fig. 3*c*, solid symbols). A shift in the shape of the distribution will shift the position of the different quantiles and accordingly the slope of the QQ plot. A removal of individuals in the lower part of the distribution (the predicted result from a negative-energy-dependent mortality) will lead to a positive increment of the lower quantiles but no change in the upper quantiles. Consequently, the slope of the QQ plot will be less than one (Fig. 3*c*, open symbols). A plot of the incremental difference between the quantiles of the initial distribution (Fig. 3*a*) and the resulting distribution (Fig. 3*b*) (QQ increment) will then result in a negative slope (Fig. 3*d*). A shift in the position of the distribution will not change the relative incremental difference between the different quantiles. The parameters of the QQ-increment slope and intercept were calculated by least square regression.

Fig. 3. Changes in quantile–quantile (QQ) plots as a result of changing the shape of the energy distribution. Removal of the individuals with the 20% lowest energy from (*a*) a simulated distribution with mean 5513 $J \cdot g^{-1}$ (±438 standard deviation, SD) results in (*b*) a distribution with the left-hand tail missing. (*c*) Plotting the resulting quantiles results in a slope of the QQ plot < 1 (solid symbols) compared with the QQ plot if no change in the shape of the distribution has occurred (open symbols). (*d*) The resulting QQ-increment plot demonstrates a negative slope.



To estimate the significance of the observed QQ increment between subsequent sampling periods, the probability of obtaining the observed QQ increment was simulated using resampling. The null hypothesis that the two samples originated from the same distribution was tested by drawing two distributions of the same size as the respective original distributions at random with replacement from both distributions pooled. The QQ-increment slopes between the resampled distributions were then calculated by least square regression. This procedure was repeated 1000 times. The significance of the observed QQ-increment slope was estimated as the frequency at which of the resampled slopes equalled, or was more negative than, the QQ-increment slope of the original comparison.

The probability of detecting changes in the energy distribution (test power) depends on both sample size and the

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Table 2. Definition of parameters used in the energetic modelling.

Parameter	Equation	Values investigated
Food consumption (C)	$C = X_0 e^{0.1697T} W^{0.766}$	X_0 = 0.28 to 28.28
Faces and excretory products ($F + U$)	$F + U = X_1 C$	X_1 = 0.31
Standard metabolism (R_s)	$R_s = (0.739T + m)\left(\frac{20}{W}\right)^{0.14}$	m = 5 to 15
Activity metabolism + SDA (R_a)	$R_a = \gamma R_s$	γ = 0.1 to 4
Probability of feeding (P_i)	$P_i = \frac{e^{b_0 + b_1 E}}{1 + e^{b_0 + b_1 E}}$	b_0 = 12.99 to 18.00 b_1 = –0.002 to –0.004
Correlation W and E	ρ_{EW}	0.06 to 0.56

Note: The shape of the energy distribution did not change in a right-hand direction (slope of the QQ increment > –0.01) within the range of parameter values investigated. W, fresh mass (g); E, specific energy (J·g^{-1}); T, water temperature, set to 0.5 during the simulation. The size scaling exponent of weight in the food consumption and metabolism function and the proportionate relationship between energy consumed and energy lost in feces and excretory products are borrowed from brown trout (*Salmo trutta*) (Elliott 1976). All energy values are quoted as J·g^{-1}·day^{-1}. SDA, specific dynamic action.

magnitude of the changes (effect size). We estimated test power as a function of sample size and effect size by resampling two distributions with replacement. Significance of the shape differences between the resampled distributions, measured as the QQ-increment slope, was estimated as described above. This procedure was repeated 250 times and the test power was estimated as the proportion of significant differences in distributions at $p < 0.05$. The sample sizes of the resampled distributions were varied from 15 to 500 and the effect sizes, being the slope of the QQ increment, were varied between $\beta = -0.15$ and –0.34. The resampled distributions originated from two of the original datasets (February–March and April–May 2002) but were manipulated to create two additional distribution datasets and range of effect sizes ($\beta = -0.15$ to –0.34).

Modelling the energy distribution

A population's energy distribution is shaped by both population-level factors (e.g., energy-selective mortality) and individual factors (e.g., metabolism or energy gain). When assessing changes in the shape of the population's energy distribution, it is therefore also important to consider other processes than mortality and the magnitude of changes that they may generate. Appetite and foraging behaviour have been shown to correlate negatively with energy reserves in juvenile Atlantic salmon (e.g., Metcalfe and Thorpe 1992). If low-energy individuals have a higher energy intake than high-energy individuals, then the fish in the lower part of the energy distribution may increase their energy content relative to fish in the upper part. This will result in an observed decrease in the frequency of low-energy individuals in the population. On the other hand, because of the expected positive correlation between specific energy content and somatic size (e.g., Post and Parkinson 2001), low-energy individuals are expected to be smaller in size and therefore to have correspondingly higher mass-specific metabolic costs. Higher metabolic costs of low-energy individuals means that fish in the lower part of the energy distribution reduce their energy content relative to fish in the upper part, resulting in an increase in the frequency of low-energy individuals, in direct contrast to changes owing to increased mortality of low-energy individuals.

In the following, we investigate the potential for changes in the energy distribution resulting from individual differences in metabolism (size scaling) and foraging (size and energy scaling) using population-specific parameters for metabolism and food consumption obtained for River Alta juvenile salmon. The change in the energy content of an individual during a given time period (ΔB) may be given as

$$(1) \qquad \Delta B = C - (F + U + R_s + R_a)$$

where C is the energy content of the food consumed, $F + U$ is the energy content of the feces and excretory products, and R_s is the resting metabolism of the fish. R_a is here set to represent both the energy cost associated with increased activity metabolism, feeding, and specific dynamic action. Below, energy values are presented as J·g^{-1}·day^{-1} fresh mass (Table 2). As a starting point for the simulations, a bivariate normal distribution of energy and mass was constructed by using values for means (± standard deviation, SD) of fresh mass (W) and energy (E), as well as the correlation between these two variables (ρ_{EW}, range 0.06–0.56) from the field samples in the River Alta.

Juvenile Atlantic salmon is known to undertake periods of energy-dependent anorexic and inactive behaviour during wintertime (c.f., Metcalfe and Thorpe 1992), and the event of an individual feeding during a given time period was simulated as a binary random variable. The event of feeding during a given time period (i) was drawn at random from a binominal distribution with the probability of feeding (P_i) set to depend on the energy status of the fish in the previous time interval ($i - 1$) (eq. given in Table 2). The relationship between P_i and energy was estimated from field data using the occurrence of food in the stomach in an individual fish as a measure of feeding activity of this fish in the period immediately before catch. The variable describing empty stomachs or stomachs with content was treated as binary response variable in a logistic regression model with energy as predictor. A significant relationship between the occurrence of stomach contents in the fish and energy was only

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detected in samples from February 2001 and March 2000 (model statistics Feb. 2001, –2 log-likelihood = 47.59, χ^2 = 5.87, df = 1, $p < 0.015$; model statistics March 2000, –2 log-likelihood = 29.02, χ^2 = 6.58, df = 1, $p < 0.010$). The parameter estimates (± standard error, SE) for b_0 and b_1 (Table 2) ranged from 12.99 (5.91) to 18.00 (8.95) and from –0.002 (0.001) to –0.004 (0.002), respectively. As indicated by the negative sign of the coefficient of energy scaling (b_1), the probability of feeding decreased with increasing energy level. Within these estimated parameter values of the energy to feeding probability relationship, P_i ranged from 0.88 to 0.99 and from 0.002 to 0.72 given energy values of 6000 and 4000 J·g^{-1}, respectively. Because negative-energy-dependent feeding represents the only plausible variable that allows low-energy individuals to obtain a higher relative net energy balance than high-energy individuals, we chose to include this in our modelling, even though foraging was found to be significantly correlated to energy levels in only a few of the investigated sampling periods.

Fresh mass was kept constant during the modelling as we assume zero growth, and the change in energy content of an individual during one time period (ΔB) is given as

$$(2)\quad \Delta B = \begin{cases} C - (F + U + R_s + R_a) & \text{with probability } P_i \\ -R_s & \text{with probability } (1 - P_i) \end{cases}$$

Parameter values for the standard metabolism (R_s) and food consumption (C) models (Table 2) were determined from experimental data using hatchery-reared first generation juvenile Atlantic salmon from the River Alta population (Forseth et al. 2000). The fish used in these experiments were acclimatised to winter conditions and the relationships between standard metabolism and temperature, as well as food consumption and temperature, were determined using simulated winter temperatures (1–6 °C) and light conditions (8 h dark and 16 h light). The estimated food consumption in laboratory (X_0; Table 2) is expected to represent a maximum energy intake (J·g^{-1}·day^{-1}), and in the following, the estimated constant (X_0 = 28.28) was varied to range between the model value and one order of magnitude less (Table 2). The constant for metabolism (m = 7.128; Table 2) was also varied within a range around the model values (Table 2). The energy cost associated with the activity of feeding and specific dynamic action (R_a) was modelled as various multipliers of standard metabolism (Boisclair and Leggett 1989) (Table 2). According to Elliott (1976), the energy lost in feces and excretory products ($F + U$) was set to depend proportionately on the amount of food consumed (C) (Table 2). The effect of the change in energy content on the energy distribution was assessed after 30 time intervals (days), which represents the time between consecutive samplings in the field part of the study.

Results

Changes in mass and energy

The dry-mass percentage to specific energy relationship proved highly significant ($F_{(1,68)}$ = 600.28, $p < 0.001$, adjusted R^2 = 0.90) (Fig. 4*a*). Including weight or sampling period into this model only marginally increased the fit (~1% increase in adjusted R^2), and no significant dry-mass percentage by weight or sampling period interaction was apparent (Figs. 4*a* and 4*b*). Weight and sampling period were therefore not included in the model. No deviations from normality or correlation between residuals and predicted values were detected.

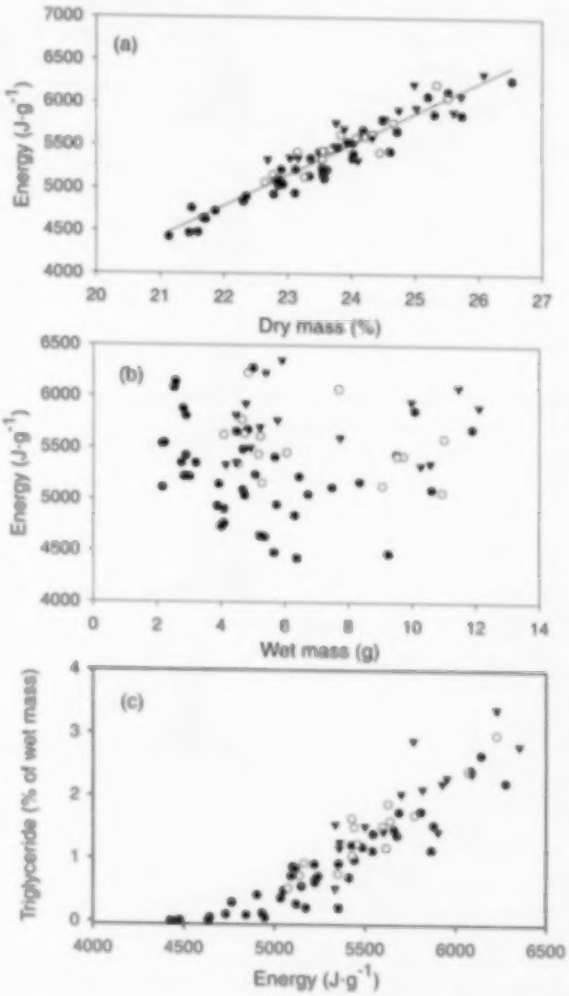

Fig. 4. Specific energy (J·g^{-1}) plotted against (*a*) dry-mass percentage, (*b*) wet mass, and (*c*) triglyceride content (% of wet mass) for juvenile Atlantic salmon (*Salmo salar*) sampled in the River Alta during January (▼), March (○), and May (●) in 2001. Least square regression line is given for dry-mass percentage to specific energy.

Specific energy content of the fish decreased during the studied winter period (Table 3; Fig. 5). With the exception of the January and February samples, specific energy content and its temporal variation was relatively similar between the 2001 and the 2002 winter periods (Fig. 5). From January to May 2001 and 2002, mean daily decrease in energy was 4.36 and 5.29 J·g^{-1}·day^{-1}, respectively. The lowest mean energy content in these years was observed in the May samples

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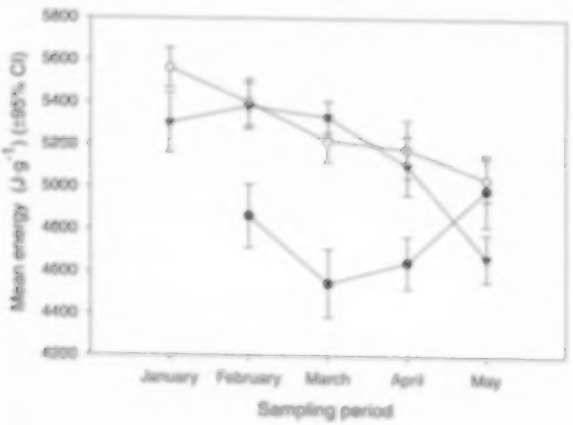
Table 3. Analysis of covariance (ANCOVA) table for the effect of sampling period and fresh mass (covariate) on energy content of juvenile Atlantic salmon (*Salmo salar*) sampled in the River Alta during the winter periods of 2000, 2001, and 2002.

Sampling year	Source of variation	df	MS	*F*	*P*
2000	Period	3	316 137	2.849	0.042
	Mass	1	858 596	7.739	0.007
	Period × mass	3	326 688	2.945	0.037
	Error	88	110 947		
2001	Period	4	1 048 803	7.799	<0.001
	Mass	1	3 659 395	27.211	<0.001
	Period × mass	4	23 634	0.176	0.951
	Error	265	134 480		
2002	Period	4	486 401	3.280	0.012
	Mass	1	148 635	1.002	0.318
	Period × mass	4	155 133	1.046	0.384
	Error	246	148 300		

Fig. 5. Mean specific energy content (±95% confidence interval, CI) for juvenile Atlantic salmon (*Salmo salar*) sampled in the River Alta during the winter periods of 2000 (●), 2001 (○), and 2002 (▼).



at 5040 J·g^{-1} (2001) and 4670 J·g^{-1} (2002). The samples from 2000 were characterised by considerably lower initial energy content and a different temporal pattern of energy depletion (Fig. 5). During the first month of this winter, mean energy decreased at 10.57 J·g^{-1}·day^{-1} down to 4547 J·g^{-1} and remained constant between the following two sampling periods before increasing from April to May. Specific energy increased with increasing fresh mass in samples from both 2000 and 2001 (Table 3). During the winter period 2002, we were unable to detect any significant relationship between fresh mass and energy (Table 3).

Triglycerides constituted from 3.4% to 0% of wet body mass of the fish (Fig. 4c). There was a strong positive linear correlation between specific energy and triglyceride content (Pearson $r = 0.91$, $p < 0.001$, $N = 70$) (Fig. 4c). Detectable levels of triglycerides were found only in individuals with specific energy content above approximately 4430–4790 J·g^{-1} (Fig. 4c).

Table 4. Intercepts (α) and slopes (β) for QQ-increment relationships between energy distributions from successive sampling periods in the River Alta winters of 2000, 2001, and 2002.

Sampling period	Intercept (α)	Slope (β)	*P*(β)
February–March 2000	–602	0.06	0.666
March–April 2000	1699	–0.35	0.025
April–May 2000	612	–0.05	0.642
January–February 2001	45	0.04	0.633
February–March 2001	–1272	0.19	0.844
March–April 2001	178	–0.04	0.460
April–May 2001	80	–0.04	0.380
January–February 2002	675	–0.11	0.244
February–March 2002	1232	–0.24	0.048
March–April 2002	–2686	0.45	0.981
April–May 2002	1383	–0.34	<0.001

Note: Significance (*P*) of the QQ-increment slope is given as the probability that parameter (β) is lower than the observed value given that the two samples are drawn from the same distribution (number of resamples = 1000).

Body size of the sampled juvenile salmon did not vary within the three studied winter periods. We were unable to detect any significant difference in mean total length (mm) between successive samples in 2000 ($F_{[3,157]} = 0.236$, all $p = 0.871$), 2001 ($F_{[4,270]} = 0.124$, all $p = 0.974$), or 2002 ($F_{[4,277]} = 0.842$, $p = 0.499$). Similarly, no significant differences in mean total fresh mass (g) were discovered between any of the successive samples in 2000 ($F_{[3,157]} = 0.135$, $p = 0.939$), 2001 ($F_{[4,270]} = 0.675$, $p = 0.610$), or 2002 ($F_{[4,277]} = 1.115$, $p = 0.349$). This was further underlined by the lack of significant changes in the distribution pattern of both total length (mm) and fresh mass (g) between any of the successive sampling periods (total length, Kolmogorov–Smirnov $Z < 1.144$, all $p > 0.146$; fresh mass, Kolmogorov–Smirnov $Z < 1.148$, all $p > 0.143$).

Changes in energy distributions

The energy frequency distribution changed significantly between March and April 2000, February and March 2002, and April and May 2002 (Table 4; Fig. 6). This change was evident by a significant negative slope of the QQ increment (β = –0.35 to –0.23) and indicated that an energy-selective process had contributed to change the shape of the energy distribution. The values of the intercept (α = 1291 to 1664) and the slope (β = –0.24 to –0.35) parameters (Table 4) indicated a positive QQ increment with negative slope, demonstrating that the number of individuals in the left-hand tail of the distribution had been reduced.

The probability of detecting differences between the energy distributions varied considerably within sample sizes and effect sizes (Fig. 7). For sample sizes commonly applied in the present study ($N > 40$), test power was reasonably high at the two largest effect sizes tested (β = –0.34 and –0.28). In contrast, test power remained low for even very large sample sizes given the lowest effect size considered (β = –0.15).

The energy modelling demonstrated that a shift of the mode of the energy distribution in a left-hand direction, corresponding to a removal of low-energy individuals, was not possible within the range of the considered parameter values

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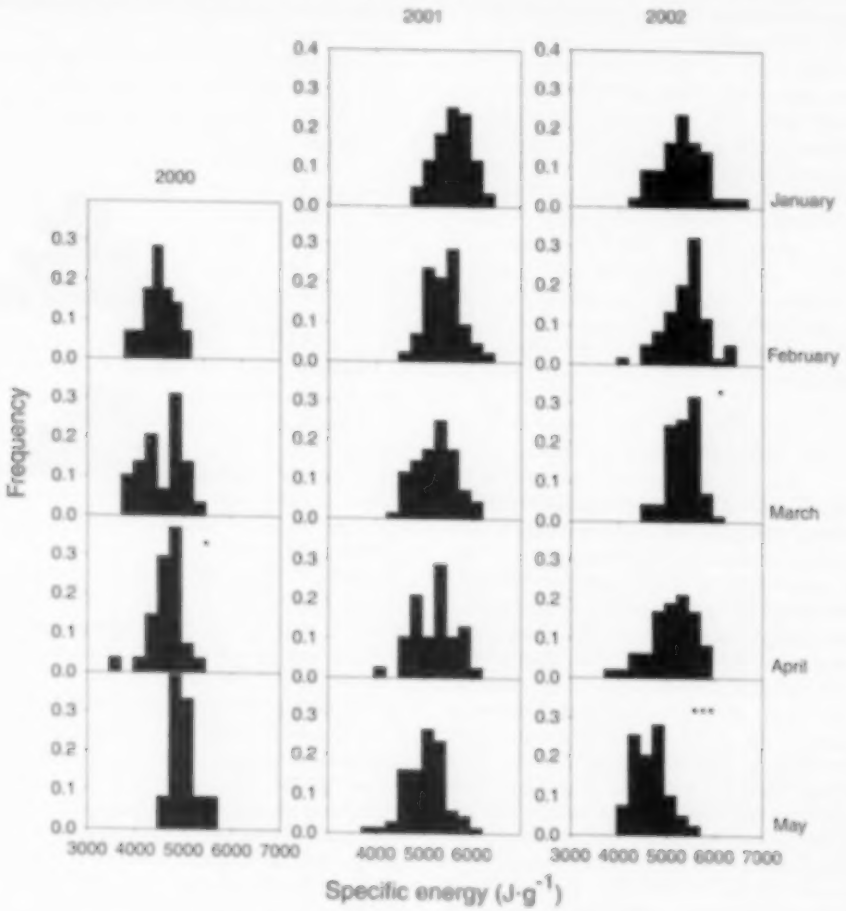
Fig. 6. Energy density distributions (specific somatic energy, J·g^{-1}) of juvenile Atlantic salmon (*Salmo salar*) sampled in the River Alta during the winter periods of 2000, 2001, and 2002. Significance of the quantile–quantile increment slope plot between the given sampling period and the previous is indicated: ***, $P < 0.001$; *, $P < 0.05$.



(Table 2). Metabolism is dependent on body mass rather than on energy. In addition to the relationship between energy and food consumption, the mass–energy correlation (ρ_{EW}) therefore proved to be the most important driving force behind changes in the energy distribution. In field samples, ρ_{EW} was found to be positive and ranged from 0.06 to 0.56. The lower tail of the energy distribution therefore consisted of comparably smaller fish than in the upper tail, implying that low-energy individuals had higher mass-specific metabolic costs. The comparable higher foraging gain of low-energy individuals did not fully compensate for the higher metabolic cost. During the simulated 30-day period, low-energy individuals lost more energy than high-energy individuals. This resulted in a prolongation of the left-hand tail in the final energy distribution. The modelled energy distribution therefore shifted in an opposite direction to the shift in the energy distributions observed in field samples (Figs. 6, 8).

The observed decreases in mean energy contents during the 2001 and the 2002 study periods, as well as between the first two sampling periods in 2000, was less than predicted by metabolic costs alone. This indicated that a net energy intake had taken place in order to defend the observed energy levels. The magnitude of this energy intake may be grossly estimated using the energetic model (eq. 2). If we assumed an activity multiplier $\gamma = 1$ and the metabolism parameter $m = 7.13$ (estimated value), the food consumption parameter (X_0) had to be set to values between 4.0 and 13.0 (depending on parameter values for b_0 and b_1) to restrict the daily energy loss to 4.36 J·g^{-1}·day^{-1} (mean energy loss during 2001). For a 6.1-g fish (grand mean of all sampling dates), this corresponded to an energy intake during a day of approximately 17–57 J·g^{-1}, or at 14%–46% of maximum food consumption estimated for laboratory fish (Forseth et al. 2000). A significant energy intake during the winter is also demonstrated from the field data by the high proportion (30%–100%) of fish with food in their stomachs.

Discussion

It is evident that a state-dependent process has acted on, and changed, the energy distribution pattern of the 2-year-

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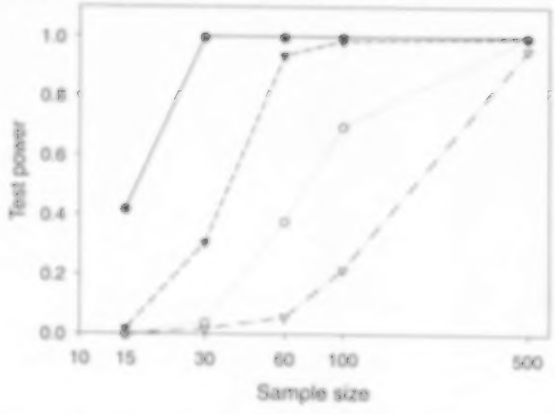
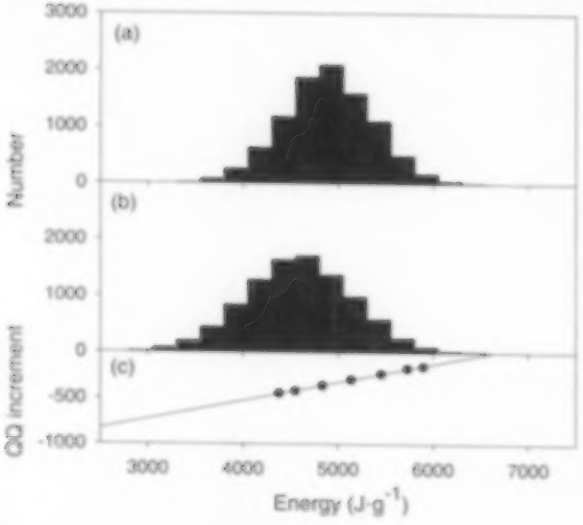
Fig. 7. The probability of detecting changes in the population's energy distribution (test power) at the 5% significance level for sample sizes ranging from 15 to 500. Investigated effect sizes (slope of quantile–quantile increment plot) was $\beta = -0.34$ (●), $\beta = -0.28$ (▼), $\beta = -0.24$ (○), and $\beta = -0.15$ (▽).



old and lower-mode 3-year-old juvenile Atlantic salmon during three of the study periods. The observed change corresponded to the removal of low-energy individuals from the population and is most likely a direct result of energy-selective mortality. Differences in catchability between individuals with different energy status may have a potential to influence the observed distributional changes. The catchability of fish by electroshocking is known to increase with fish size (Bohlin et al. 1989). However, small between sampling period variation in size indicates that the direct physiological vulnerability to electroshocking did not vary significantly. Moreover, when the influence of energy status on behaviour is investigated for Atlantic salmon parr in wintertime, low-energy individuals are found to have a comparably higher activity level (e.g., Simpson et al. 1996; Bull et al. 1996; Metcalfe and Thorpe 1992). This indicates that low-energy individuals are expected to be more vulnerable to sampling. Accordingly, our observations of the disappearance of low-energy individuals from the population are not expected to be generated by sampling bias.

One of the main problems related to the use of distributional statistics to infer state-dependent mortality is that other processes may act on and change the distributions. For example, within-population differences in growth rate may change the population's size distribution and interfere with attempts to use these to detect size-dependent mortality (e.g., Munch et al. 2003). In the present study, we control for non-mortality-induced changes in the energy distribution using energetic modelling. This approach demonstrated that metabolism and energy-state-dependent foraging was not likely to generate the observed changes in the energy distribution. The variables in the bioenergetic model were deliberately varied within wide ranges to make the results more robust to erroneous parameterisation resulting from, e.g., differences between laboratory and field conditions. Changes in model parameters and biases resulting from erroneous parameterisation are therefore unlikely to alter our conclusion. Despite a considerable decline in energy content, only minor changes in size (measured as body mass or length) was observed during the studied winter periods. This indicates that the observed changes in the energy distribution are relatively independent of size. However, the size range was relatively limited in the present study.

Fig. 8. (*a*) Simulated energy frequency distribution with mean energy 5136 $J \cdot g^{-1}$ (± 460 standard deviation, SD) and (*b*) resulting energy frequency distribution after modelling the energy budget during 1 month for individual fish. Mean of the underlying weight distribution was set to 6.7 (±2.9 SD) and $\rho_{BW} = 0.13$. (*c*) The resulting quantile–quantile (QQ) increment with slope = -1.07×10^{-19} and intercept = 3.84×10^{-14}. Parameter values: $P = 0.5$, $\gamma = 1$, $M = 10$, $X_0 = 7.4$, $b_0 = 18.00$, and $b_1 = -0.004$.



The few studies investigating stream-living salmonids under winter conditions univocally report a decrease of storage energy during wintertime. Cunjak (1988) reported a rapid depletion of fat resources in early winter, with a further depletion later in winter for brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in Canadian rivers. Berg and Bremset (1998) determined seasonal variation in proximate composition of juvenile Atlantic salmon and brown trout in the River Humla, Central Norway. In this study, specific fat content was reduced by 45% to 70% during winter, and the fish had their lowest tissue concentrations of lipids in April, with a mean content of stored non-polar lipid of 600 $J \cdot g^{-1}$ (Berg and Bremset 1998). Hutchings et al. (1999) recorded similar levels of lipid content in reproductive male brook trout after 7 winter months in a stream.

Depletion of energy has previously been suggested as a major cause of winter mortality in juvenile temperate fishes (Gardiner and Geddes 1980; Post and Evans 1989; Miranda and Hubbart 1994). However, to our knowledge, we are the first to demonstrate a change in the energy distribution of juvenile Atlantic salmon during wintertime and to link this to selective removal of low-energy individuals from the population. Evidence for energy-selective winter mortality has previously been based on more indirect measures. Periods of rapid energy depletion have been found to coincide with events of high mortality (Gardiner and Geddes 1980) or periods of size-dependent mortality have been linked to the

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comparable lower levels of storage energy in small fish (e.g., Miranda and Hubbard 1994; Post and Evans 1989).

A critical level of lipid content necessary for survival has been demonstrated in laboratory experiments with yellow perch (*Perca flavescens*) (Newsome and Leduc 1975). The primary energy storage molecule in fish is the lipid class triglycerides (Sheridan 1988). Measures of lipid class composition from juvenile Atlantic salmon from the River Alta indicates that triglycerides may be present in the fish at energy levels as low as 4430–4790 J·g^{-1}. Interesting, it is apparent from visual inspection of Figs. 4 and 6 that the lower limits of the energy distributions observed during wintertime in the River Alta seems to correspond fairly well with the lower limits of storage lipids. Further, in two of the instances when energy-selective mortality was detected (March to April 2000 and April to May 2002), the left-hand tail of the energy distribution in the first of the two compared sampling dates was considerably lower than 4500 J·g^{-1}. The lowest energy level recorded during the present study was in the March and April 2000 samples, with mean energy as low as 4570 J·g^{-1}. The only period with an increase in mean energy content was between April and May 2000. Although the sample size in May 2000 is too small to make statistical inference advisable, the sample is included in the study for illustrative purposes: the right-hand tail of the distribution remains fairly constant both in shape and position and illustrates how an observed increase in mean energy may be due to a disappearance of low-energy individuals (approximately <4500 J·g^{-1}). In summary, our study indicated that Atlantic salmon parr have a lower energy threshold for winter survival and that this threshold corresponds to a depletion of triglycerides.

Both temperature and water discharge remained fairly stable throughout the study periods. This was mainly due to hydropower regulation, operated at a constant flow rate throughout the winter, where the outlet water from the water reservoir is located just above the sampling area. The slope of the QQ increment was negative in seven of the 11 month-to-month comparisons. A negative slope is expected if energy-selective mortality occurs. We were only able to demonstrate significant energy-dependent mortality in three of the comparisons. This should, however, not be interpreted as evidence that energy-dependent mortality is not occurring. Although our test procedure has a high probability of detecting the largest changes in the energy distributions, small changes are unlikely to be detected because of low test power, even for very large sample sizes. There were, however, periods with sufficient test power where we did not detect significant mortality. This indicates that energy-dependent mortality is an episodic rather than continuous process. Although we were not able to detect any links between environmental factors and variation in mortality, such relationships may exist, and indeed even the lower limits of energy or storage lipids necessary for survival may not be constant but co-vary with environmental factors.

Juvenile Atlantic salmon in the River Alta depend on a significant energy intake during wintertime to maintain energy levels above the threshold where triglycerides are depleted. These findings correspond with estimates of the winter energy budget from the River Humla, where Berg and Bremset (1998) concluded that foraging during wintertime contributed up to 50% of the salmon parr energy demand. It has previously been demonstrated by experimental studies and modelling that depletion in storage energy of juvenile Atlantic salmon may be a counterbalance between behavioural tactics shifting between anorexia or feeding (Metcalfe and Thorpe 1992; Bull et al. 1996; Valdimarsson and Metcalfe 1998). This relationship has been suggested to be caused by a combination of increased foraging risk during wintertime, resulting from impaired swimming performance at low water temperatures, and less energetically profitable feeding. As demonstrated by experiments, the timing of anorexia is under photoperiodic control (Metcalfe et al. 1986; Villarreal et al. 1988), but the extent of the loss of appetite is influenced by energetic status (Metcalfe and Thorpe 1992). This suggests that the fish regulate appetite to maintain energy reserves above a threshold (Bull et al. 1996). The results from the present study point to a lower energy limit necessary for survival in juvenile Atlantic salmon. However, it is not possible to draw conclusions regarding the underlying mechanism. Although energy deficiency may be the governing force behind the observed mortality pattern, the causal mechanism does not necessarily involve nutrition shortage and starvation. An increase in activity level of the fish to defend certain energy levels may increase predation risk, as well as vulnerability to physical stress caused by biotic factors. Thus, the suggested energy limit may be indirectly set through increased risk-taking behaviour in low-energy individuals and vary concordantly with environmental variables.

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Factors affecting marine production of Atlantic salmon (*Salmo salar*)[1]

Bror Jonsson and Nina Jonsson

Abstract: This paper reviews recent advances in our understanding of factors influencing the marine production of wild Atlantic salmon (*Salmo salar*). Population abundance has declined during the last 30 years because of decreased marine growth rate, survival-rate, and production of multi-sea-winter fish. Mortality appears density-independent, indicating that the marine abundance is beneath the carrying capacity for the species. Correlations between the North Atlantic Oscillation winter index for the post-smolt year and production variables indicate that unfavourable climatic conditions are partly responsible for the decline. Low sea temperature may be the ultimate reason for the poor salmon production, whereas predation is one proximate mortality factor, which is probably both size and temperature dependent. Low growth rate during cold years was associated with low sea age at maturity and small salmon, contrary to the common observation that fast growth leads to young age at maturity. It is suggested that low water temperature may stimulate lipid storage relative to protein production and that the energy density needed to attain sexual maturity is lower in small than in large salmon. Future research should focus on the relationships between smolt age and (or) size and adult age and (or) size, and the association among water temperature, growth rate, growth efficiency, and age at sexual maturity.

Résumé : Nous présentons une synthèse des découvertes récentes sur la compréhension des facteurs qui influencent la production en mer des saumons atlantiques (*Salmo salar*) sauvages. L'abondance des populations a baissé au cours des 30 dernières années à cause de la réduction du taux de croissance en mer, du taux de survie et de la production de poissons qui passent plusieurs hivers en mer. La mortalité ne semble pas liée à la densité, ce qui indique que l'abondance en mer est inférieure au stock limite de l'espèce. Les corrélations entre l'indice d'hiver de l'oscillation nord-atlantique dans l'année qui suit la transformation en saumoneau et les variables de la production indiquent que les conditions climatiques défavorables sont en partie responsables du déclin. Les températures basses de l'océan peuvent être la cause fondamentale de la production réduite de saumons, alors que la prédation est un facteur immédiat de mortalité qui varie probablement en fonction tant de la taille que de la température. La croissance réduite durant les années fraîches est associée à une maturité à un âge en mer bas et à des saumons de petite taille, contrairement à ce qu'on observe ordinairement qui est qu'une croissance rapide mène à une maturité à un âge précoce. Nous formulons les hypothèses suivantes selon lesquelles la température basse de l'eau peut stimuler l'accumulation de graisses plutôt que la production de protéines et la densité énergétique requise pour atteindre la maturité sexuelle est plus basse chez les petits saumons que chez les grands. Les études futures devront considérer les relations entre l'âge/taille des saumoneaux et l'âge/taille des adultes, ainsi que l'association entre la température de l'eau, le taux de croissance, l'efficacité de la croissance et l'âge à la maturité sexuelle.

[Traduit par la Rédaction]

Introduction

Studies indicate that the production of wild Atlantic salmon (*Salmo salar*) has decreased gradually over the last 30 years (Parrish et al. 1998; Scott 2001; Klemetsen et al. 2003), and concern is increasing over the continued decline (B. Jonsson et al. 1999; Potter and Crozier 2000; Friedland et al. 2003). The reported salmon catch in the North Atlantic has decreased from approximately 13 000 tonnes in 1973 to 2000 tonnes in 1999 (Scott 2001), and the reported return rate of tagged fish in, for instance Norway, has been reduced to about one tenth of what it used to be in the 1970s (Friedland 1998). However, the lower catch may result from both reduced marine fishing intensity with banning of the Norwegian drift net fishery and strong reduction of the Faroese long-line fisheries, as well as lower marine survival of salmon.

The production of each cohort (P_t) during the time period t is determined by the size (biomass) of the smolt year class (B_0) from which the cohort is recruited, the instantaneous

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B. Jonsson[2] and N. Jonsson. Norwegian Institute for Nature Research, Dronningensgt 13, P.O. Box 736, Sentrum, N-0105 Oslo, Norway.

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[2]Corresponding author (e-mail: bror.jonsson@nina.no).

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marine growth rate (g_t), and the instantaneous mortality rate at sea (Z_t): $P_t = g_t B_0[\exp(g_t - Z_t) - 1]$ (Wootton 1998). Thus, the production is positive when $g_t > Z_t$ or $g_t/Z_t > 1$, where $g_t = (\ln S_a - \ln S_s)/t$, S_a is adult size, S_s is smolt size, $Z_t = (\ln N_s - \ln N_a)/t$, and N_a is number of adults produced from N_s smolts. Hence, the production P_t is positive when $(\ln S_a - \ln S_s)/(\ln N_s - \ln N_a) > 1$, and the temporal development in salmon production can be judged from the relationship between the size increment and numbers lost at sea.

Fluctuations in annual production of marine fishes are often related to climatic variation (Cushing 1982). Abundant year classes are produced in years when the feeding opportunities are good at the time that fish start to eat, and poor cohorts are produced when food is scarce at the time that fish start feeding (match–mismatch hypothesis). This hypothesis is supported by investigations on the survival of fish larvae from species as different as anchovies (*Engraulis capensis*) (Plaganyi et al. 2000), blue whiting (*Micromesistius poutassou*) (Hillgruber and Kloppmann 1999), and radiated shanny (*Ulvaria subbifurcata*) (Dower et al. 2002). In cod (*Gadus morhua*), climatic factors are important not only for eggs and larval stages, as stated by the match–mismatch hypothesis, but also for larger juveniles (Brander et al. 2001; Fromentin et al. 2001). Possibly, a similar relationship holds for juvenile salmon entering the sea as smolts (Andreassen et al. 2001), as maintained for pink salmon (*Oncorhynchus gorbuscha*) (Willette 2001). For Atlantic salmon, marine production is linked to sea survival (Hansen and Jonsson 1991; McCormick et al. 1998), their initial size (McGurk 1986; Pepin 1991), the fishing intensity (Windsor and Hutchinson 1990), and climatic factors in the ocean that influence feeding opportunities and predation risk (Friedland et al. 1998; N. Jonsson and B. Jonsson 2003).

The North Atlantic Oscillation index (NAOI) is one of the main indices of the climate in the Northern Hemisphere. This index gives the atmospheric mass balance between the subtropic atmospheric high-pressure zone centered over Ponta Delgada, Azores, and the atmospheric low pressure zone over Stykkisholmur, Reykjavik, Iceland (Hurrell 1995). A high or positive winter NAOI corresponds with mild winter climate and strong storms in western Europe. A low index accords with weaker winter storms and lower air temperature. Off north Norway, however, the current of warm Atlantic water and ultimately the temperature in the Barents Sea is found to decrease with high winter NAOI (Ådlandsvik and Loeng 1991; Dickson et al. 1999). Helle and Pennington (1999) have shown that zooplankton abundance along the Norwegian coast increases with increasing inflow of warm Atlantic water, with trophic effects mediated through the food chain. Apart from the direct regional effect of NAO on surface circulation, it affects large-scale convection activity in the North Atlantic and is responsible for changes in the circulation of water (Dickson 1997; Dickson et al. 2002). For instance, the thermal habitat of Atlantic salmon (i.e., the size of the area with relatively warm surface water) has fluctuated in parallel with changes in NAOI (Friedland et al. 1998; Dickson and Turrell 2000), decreasing in years of positive NAOI and expanding during negative phases of oscillation, opposite to what might be expected from the air temperature pattern in northwestern Europe. The NAOI has to a large extent been positive during the most recent 30 years and has correlated with fluctuations in production traits of marine and freshwater animal populations, as well as in terrestrial animals and plants (Post and Stenseth 1999; Ottersen et al. 2001), Atlantic salmon included (N. Jonsson and B. Jonsson 2004).

This paper reviews factors influencing marine production of Atlantic salmon as described above. The marine life of salmon was recently reviewed by Hansen and Quinn (1998) and Friedland (1998). Our aim is not to repeat the evidence presented in these recent reviews, but to extend the knowledge to the present state of the art. To complement the picture, however, we have included some older information and information on other fish species, when appropriate.

Recruitment and density-independence

Fisheries theory assumes that the mortality of salmon in the ocean is density-independent (Charnov 1986). The rationale behind this is that the population density is far below the assumed carrying capacity for salmon in that habitat. For Atlantic salmon, N. Jonsson et al. (1998) found that the number of adults in the Norwegian River Imsa increased linearly with the annual number of smolts recruiting to the cohort: the higher the average smolt output, the higher the average number of returning spawners from the cohort. For the smolt cohorts from 1976 to 1994, the total number of recaptured adults increased with a factor of 0.3 of the number of seaward-migrating smolts ($r^2 = 0.73$, $p < 0.001$); for those returning to the River Imsa for spawning, the corresponding factor was 0.078 ($r^2 = 0.38$, $p < 0.01$). One might have expected positive density-dependence (e.g., owing to increased navigational accuracy; B. Jonsson et al. 2003) or increased survival with increased salmon abundance owing to a functional response of the potential predators (Wood and Hand 1985). There was, however, no support for such effects in the River Imsa salmon, indicating that the recruitment rate is below the carrying capacity for wild Atlantic salmon in the North Atlantic and that salmon production increases proportionally with the recruitment rate.

Although there may be no similar density-independent marine mortality rate in Pacific salmon (*Oncorhynchus* spp.) (McKinnell 1995; Bigler et al. 1996), density-independent factors are widely believed to be important contributors to variation in population abundance of these species as well. Peterman (1981), for example, gave evidence for density-independent marine survival in the Oregon coho salmon (*Oncorhynchus kisutch*), and variation in the ocean climate may be the prime determinant of the annual changes in marine mortality (Frank and Leggett 1994). Similarly, the productivity of sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay appears to be strongly related to fluctuations in climate (Adkison et al. 1996), and the major changes in climate over the Pacific ocean in the winter of 1976–1977 apparently resulted in a change in productivity of the Fraser River sockeye salmon (Francis and Hare 1994; Beamish et al. 1997; Bradford 1999). Furthermore, analyses of lake sediments from the last 2200 years indicate climate-related changes in sockeye salmon abundance in periods before major fisheries influenced populations (Finney et al. 2002). Warm, dry years, often associated with La Niña events tend to be associated with below-average salmon survival (Mote et al. 2003).

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Table 1. Marine survival of juveniles from smolts to first-time spawning and adults from first- to second-time spawning in Atlantic salmon (*Salmo salar*).

Life history period	Variability	Source
Smolts to adults		
Western Arm Brook, Newfoundland	3%–12%	Chadwick et al. 1978
River Bush, Northern Ireland		Crozier and Kennedy 1999
To coast	14%–21%	
To river	2%–10%	
River Imsa, Norway		N. Jonsson et al. 1998
To coast	30%	
To river	7.8%	
From first- to second-time spawning		
Norwegian rivers	2%–25%	N. Jonsson et al. 1991*a*
River Teno, Finland	17.3%	Erkinaro et al. 1997
Magaguadavic River, New Brunswick	14.3%	Martin 1984
England and Wales	5%	Mills 1989
Shannon River, Ireland	7.3%*	Went 1964

*By weight.

Thus, a climatic influence on anadromous Pacific salmon is documented, as it is for several marine fish species (e.g., Noakes et al. 2000; Zhang et al. 2000; Ottersen et al. 2001).

The lower the smolt output, the fewer adults are produced. However, only a part of the variability in salmon production is explained by variation in smolt production. For the River Imsa stock, 38% of the annual variance in numbers returned was explained by this factor alone, meaning that 62% are unexplained and due to other causes. There are no similar estimates for wild Atlantic salmon from other rivers, so we cannot judge to what extent this is applicable to Atlantic salmon populations.

Sea survival

Smolt size and time of sea entry

Marine survival, from smolts to adults returning to their spawning river, appears in most cases to be less than 10% (Table 1). Mortality is viewed as highest during the first year at sea (Chadwick 1987; Hansen and Quinn 1998), and it appears to decrease with smolt size in salmon with similar sea age (Lundqvist et al. 1994). Higher survival of large smolts may result from improved escapement from size-selective predators. Thus, fish should survive better in years with relatively large smolts, which should be the effect of the preceding growth conditions for the parr in fresh water (Klemetsen et al. 2003).

Smolt age, on the other hand, may have a contrasting effect. The survival of 1- and 2-year-old hatchery smolts released in the wild is similar, although the 2-year-olds may be about five times heavier than the 1-year-olds (N. Jonsson et al. 2003). Furthermore, Chadwick et al. (1978) found higher survival to 1-sea-winter (1SW) adults for salmon entering seawater as young rather than old smolts. The survival of 3-year-old smolts was twice as high as that of 4-year-old smolts and four times higher than that of 5-year-olds. Thus, body size is not the only factor influencing sea survival of salmon.

The time when the smolts enter seawater appears to influence subsequent sea survival (Andreassen et al. 2001). Release experiments with hatchery-reared salmon revealed that survival was highest for fish entering seawater in spring (Hansen and Jonsson 1989). Fish entering sea water at other times of the year survived less well, and they strayed more to rivers farther away from their home stream when they returned for spawning, which may add to the observed smaller survival rate (Hansen and Jonsson 1991). Possibly, there is a narrow survival window in spring that should be met by the outward-migrating fish to survive well at sea (Staurnes et al. 1993; McCormick et al. 1998, 1999). The fact that large smolts move to sea earlier in the season than smaller smolts (N. Jonsson et al. 1990; Bohlin et al. 1996) may thus lead to differential survival rates of differently sized smolts. Similarly, the survival rate of coho salmon was highly influenced by the environmental conditions at the time when the smolts entered seawater (Hobday and Boehlert 2001), in accordance with the match–mismatch hypothesis.

Climate

Smolt age decreases with latitude in Europe from 4–5 years in the coldest northern rivers to 1–2 years in the south (Metcalfe and Thorpe 1990). This gradient is mainly linked to climate, with faster freshwater growth in the temperate and warm rivers than in the farther northern rivers. In southern Europe, however, juvenile growth rate may be constrained by high water temperature in the rivers (Jensen et al. 1989; Ojanguren et al. 1999; Forseth et al. 2001), with the effect that smolts are not as young as one might expect from the clinal variation farther north (Metcalfe and Thorpe 1990).

Sea survival appears influenced by the temperature in coastal waters at the time when the smolts enter seawater. Friedland et al. (2000) showed that high sea surface temperatures along the Norwegian coast during May correlated positively with post-smolt survival in Norway and Scotland. Furthermore, there is positive correlation between the size of the area with water temperature of 8–10 °C in May, when the smolts at this latitude enter the sea, and the survival of salmon (Friedland et al. 1998). A reciprocal negative correlation was found between survival and the size of the North Atlantic surface area with water temperature between 5 and

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7 °C in May. However, no significant correlation between post-smolt survival and any of the spring indices of NAO has yet been found (Jonsson and Jonsson 2004).

Predation and parasites

Evidence suggests that large parts of salmon cohorts are lost to predation during river descent and the first weeks of their marine sojourn, when both sea birds such as gulls (*Larus* spp.) and gannets (*Morus bassanus*) and fish such as cod feed on post-smolts (Hvidsten and Møkkelgjerd 1987; Salminen et al. 1995; Dieperink et al. 2002). For instance, Hvidsten and Lund (1988) found that approximately 25% of the salmon tagged as smolts were eaten by cod in the estuary during the first week after they left the River Orkla, Norway. Montevecchi et al. (2002), who had studied the amount of post-smolts landed by gannets over 24 years in a large colony off northeast Newfoundland, found that this predation took 0.3% of the smolts before 1990 and 2.5% between 1990 and 2000.

Less is known about predation during winter, but as an ectotherm, salmon may be particularly vulnerable to homoiotherm predators like whales and seals at that time, and Shearer (1992) maintained that grey seal (*Halicochoerus grypus*) may be an important salmon predator. Also, from Pacific salmon, it is known that predation by killer whales (*Orcinus orca*) as well as seals may be high (Nichol and Shackleton 1996; Zamon 2001).

All in all, marine salmon predation is probably very important for salmon survival (Moring et al. 1999). However, this is poorly understood, largely because of a lack of basic knowledge about the post-smolt distribution and habits (Friedland 1998) and also because marine predation is difficult to study owing to the low density of Atlantic salmon in the ocean.

The greatest diversity of salmon parasites is known from the marine phase, and sea lice (*Lepeophtheirus salmonis*) is one possible mortality agent present on Atlantic salmon in the ocean (Jacobsen and Gaard 1997; Butler 2002). The chances of sea lice infections have increased with the growth of the fish farming industry, and experiments with sea lice on post-smolts have shown higher mortality and lower growth rate at high rates of parasitization (Scott 2001). However, conclusive evidence on the significance for wild salmon mortality of this or other marine parasites is lacking (Bakke and Harris 1998).

Distribution

Salmon feed in the North Atlantic whether originating in south or north European rivers (Hansen et al. 1993; Hansen and Jacobsen 2003). Apparently, Atlantic salmon originating from most areas of the distribution range feed for some time north of the Faroe Islands between Norway and Greenland (Hansen et al. 1999; Holm et al. 2000; Jacobsen et al. 2001), but there are also salmon feeding west of Greenland originating from both North American and European rivers (Reddin and Friedland 1999).

Atlantic salmon stay at sea for 1–3 and sometimes 4 years before maturing and returning to the home river (Hansen et al. 1993; Erkinaro et al. 1997). The shorter their marine stay, the higher the chance of survival and return (N. Jonsson et al. 1991*a*, 2003). Furthermore, the rate of straying to foreign rivers appears to increase with the duration of the marine migration, which may be misjudged as mortality (B. Jonsson et al. 2003). The extent to which 1SW and 2SW fish share feeding areas during their first winter in the ocean is unknown (Jacobsen et al. 2001), but the marine distribution of steelhead trout (*Oncorhynchus mykiss*) varies by age and size (McKinnell et al. 1997), and it is reasonable to expect that Atlantic salmon also segregate partly by age and by size in the ocean, as juvenile salmon do during feeding in fresh water (Heggenes et al. 1999, 2002).

Salmon farming

Escaped farmed fish may impact the survival of wild stocks, not only through the spread of parasites and contagious diseases, but also through competition, hybridization, introgression, and disruption of locally adapted gene complexes (Crozier 1993; Fleming et al. 2000). Cultured salmon are subject to both artificial and natural selection in the culture environment (Gross 1998). Artificial selection occurs in crossbreeding and selective-breeding programmes aimed at improving performance traits in the culture environment (Gjedrem et al. 1991). In addition, manipulation of sex and ploidy occurs, and transgenic techniques sometimes used (Cross 2000) and the physiology of the fish may be changed (Fleming et al. 2002).

Genetic effects following releases of hatchery fish may be positive, neutral, or negative (Hindar and Jonsson 1995), but current knowledge about salmonids suggests the latter outcome to be most probable (Allendorf and Utter 1979; Hindar et al. 1991; Cross 2000). Experimental evidence of Atlantic salmon invading a natural salmon stream in Norway showed that native production and lifetime reproductive success of the native fish was depressed (Fleming et al. 2000).

Stocking of hatchery fish and escapement from fish farms can have similar effects on wild populations (Crozier 1998; Levin and Williams 2002). Interbreeding with wild fish may lead to changes in behaviour (Fleming and Einum 1997; Einum and Fleming 1997; review in B. Jonsson 1997), demographic parameters, growth, and smolt production (Hindar and Jonsson 1995; Fleming et al. 2000). Interbreeding may also reduce intra- and inter-population genetic variability (Hindar et al. 1991), which may lower the disease resistance and the buffering capacity against environmental changes (Clifford et al. 1998). Escaped hatchery fish interbreed with wild salmon both as parr (Garant et al. 2003) and adults (Fleming et al. 1996, 1997). Furthermore, high incidences of salmon × trout hybrids have been recorded in rivers situated near intensive salmon farming industry (Matthews et al. 2000). Also, in steelhead trout, the presence of hatchery fish appears to reduce the productivity of co-existing wild spawners (Chilcote 2003).

From coho salmon, there is evidence that large numbers of hatchery-produced smolts in lower rivers and estuaries attract predators (Nickelson 2003). The production of wild coho in 12 Oregon coastal rivers and two lakes was negatively correlated with the average number of conspecific hatchery smolts in each basin, but not with the habitat quality. Large numbers of hatchery smolts in Atlantic salmon rivers may also have negative effects on the production of wild fish, as assumed for coho salmon (Nickelson 2003). Furthermore, the survival of wild chinook salmon is nega-

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tively associated with hatchery releases of steelhead, and it is claimed that industrial-scale production of hatchery fish may hinder the recovery of threatened salmonids (Levin and Williams 2002). Thus, there is reason to believe that the effect of escapement from fish farms is mainly negative for wild salmonids (Ryman and Utter 1987; Hindar and Jonsson 1995; Fleming et al. 2000).

Growth

Because salmon are obligate ectotherms, ambient temperature has a pervasive controlling effect on their rate of growth and food consumption. Young Atlantic salmon in fresh water start growing at temperatures from <1 °C (Higgins 1985) to a maximum at 17–21 °C (Forseth et al. 2001; B. Jonsson et al. 2001). There is no similar observations for Atlantic salmon in the marine environment, but there is reason to believe that food consumption and growth rate will increase with summer temperature in the North Atlantic, which is the feeding area for most salmon populations in Europe (Martin and Mitchell 1985; Scarnecchia et al. 1991; Hansen et al. 1993) and North America (Saunders et al. 1983; Friedland et al. 1993), including salmon from southern Europe (Jacobsen et al. 2001).

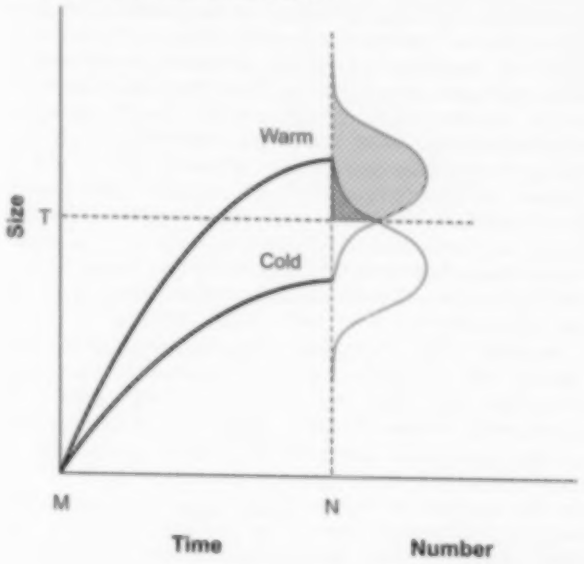
Studies of Atlantic salmon in Norway have revealed that there was positive correlation between the NAOI for May and the mass increment during the sea sojourn of 1SW salmon, but not for older fish (N. Jonsson and B. Jonsson 2004). It is reasonable to assume that the sea temperature at the time when the fish enter salt water influences the growth opportunities of the fish (B. Jonsson et al. 2001). Friedland et al. (2000), studying salmon in one Norwegian and one Scottish river, found that the higher the sea temperature during the first weeks when the post-smolts fed at sea, the larger they became. Thus, climatic conditions at the time of the marine sojourn may be important for later performance and ultimately the size of the spawners and thereby their reproductive success. The extent to which sea temperature influences first year growth of salmon from southern rivers at the time when the smolts enter the ocean is unknown.

Post-smolt growth may influence marine predation risk (Willette et al. 2001). Friedland et al. (2000) found that there is positive correlation between growth rate and survival for salmon from the Rivers Figgjo and North Esk, which they assumed was due to decreased predation rate with increasing fish size. For other rivers, such as the River Imsa, there was no significant correlation among sea growth, survival, and climatic indices for 2SW fish (N. Jonsson and B. Jonsson 2004). We feel that this is because the fish must attain a certain size at the end of their first summer to remain immature for 1 more year (N. Jonsson et al. 2003) and not because there is a link among growth rate, predation risk, and climate as hypothesized for coho salmon by Beamish and Mahnken (2001).

Age at maturity

Fast juvenile growth rate tends to decrease age at maturity relative to slow juvenile growth (Alm 1959; Reznick 1993; Day and Rowe 2002). This holds for male salmon parr in rivers (Thorpe 1986), and in sea-ranching experiments with Baltic salmon, Salminen (1997) found that sea age at first maturity was inversely related to both marine and freshwater growth rates. Good juvenile feeding opportunities gave relatively more 1SW salmon than areas with poor feeding conditions.

Fig. 1. More fish (number, hatched area) surpass the size threshold (*T*) needed to become 2-sea-winter (2SW) fish when the sea is warm during the first summer (May (M) to November (N)) at sea. The sketch is based on data from Nicieza and Brana (1993) and N. Jonsson et al. (2003).



In apparent contrast with this, Nicieza and Brana (1993) found that 2SW Atlantic salmon from two Spanish rivers had greater growth increment during their first year at sea than that of those maturing as 1SW salmon. However, in a third river, they found no significant difference in juvenile growth rate at sea between 1SW and 2SW salmon. Twenty years of Atlantic salmon monitoring in the River Imsa has similarly revealed that high growth rate during the first year at sea give relatively more 2SW and fewer 1SW salmon than cohorts with poorer growth at this life stage (N. Jonsson et al. 2003). This may be illustrated (see Fig. 1) to indicate a link between sea age at maturity and marine growth rate, and possibly with ocean climate, as found by Nicieza and Brana (1993) and N. Jonsson et al. (2003). The relationship between growth rate and sea age at maturity parallels the finding that niche shifts resulting in increased growth rate, such as the change from invertebrate to fish feeding, appear to delay maturation in salmonids (B. Jonsson et al. 1984, N. Jonsson et al. 1999). The same appears to occur when smolts of brown trout (*Salmo trutta*) go to sea; fast-growing individuals tend to attain maturity at an older sea age than slower-growing fish (B. Jonsson 1985; B. Jonsson and N. Jonsson 1993).

In their review, Hutchings and Jones (1998) noted that there is positive association between growth rate at sea and age at maturity among populations, as multi-SW populations grow generally faster than 1SW populations, contrary to the within-population tendency of early maturation of fast-growing fish (Alm 1959; Day and Rowe 2002). This finding

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has been judged as an inherited variation among populations for this trait (B. Jonsson et al. 1991), and based on their modelling work, Hutchings and Jones (1998) claimed that fast growers should usually mature younger than slow growers, unless mortality is size dependent. Decreased mortality with increasing fish size makes it more profitable to delay maturation for fast relative to slow growers. Furthermore, there may also be a link between pre-smolt growth in fresh water and age at maturity. Salmon that grow quickly in fresh water appear to do poorly at sea, and vice versa (N. Johnsson et al. 1997; Einum et al. 2002). Hence, initially fast-growing salmon may do less well during the first year at sea and attain maturity as 1SW fish, whereas those that do less well in fresh water may grow well at sea and delay maturity and become multi-SW fish (B. Jonsson and N. Jonsson 1993; Hi and Steward 2002). Thus, there may also be a positive association between fast pre-smolt growth and early sea age at maturity.

Reaction norms (a function relating an environmental variable to the phenotype expression by a genotype (Angilletta et al. 2003)) have become a unifying concept in evolutionary biology. (*i*) Early maturation and initial fast growth (which soon may level off because of shortage of food) and (*ii*) late maturation and persistently good growth are two examples of such norms in fish ecology. Both combinations of immature growth rate and age at maturity are expected to maximize fitness (Stearns 1992). The first is commonly observed among male parr in rivers (Thorpe 1986; Silverstein et al. 1997; Day and Rowe 2002), whereas the other is seen in brown trout (N. Jonsson et al. 1999) and Arctic charr (*Salvelinus alpinus*) (B. Jonsson et al. 1988), which change from invertebrate- to fish-feeders, and in Atlantic salmon from south and north Europe, mentioned above (Nicieza and Brana 1993; N. Jonsson et al. 2003). Reaction norms can differ between sexes, as they exhibit different relationships between fitness and body size (Fleming 1996), and there is usually different migratory tendencies and age and size at maturity between the two sexes of Atlantic salmon, with a larger and less variable female than male adult phenotype (B. Jonsson and N. Jonsson 1993; Presa et al. 1996).

The mechanism initiating steroid production and sexual maturity is not known in salmon, but high fat content during autumn and winter may stimulate the maturation process in Atlantic salmon (Rowe et al. 1991; Thorpe et al. 1998) as in other salmonids (e.g., Adams and Huntingford 1997; Silverstein et al. 1997, 1998). According to Thorpe and Metcalfe (1998), juvenile male salmon in fresh water (parr) will mature if genetically determined performance thresholds such as the level of energy reserves (lipids) are met in the autumn, about 1 year prior to spawning. But the maturation process may be turned off during winter if too much energy is spent at that time (Thorpe et al. 1998). Since anadromous salmonids also need large energy reserves for reproduction (Glebe and Leggett 1981; Jørgensen et al. 1997; Hendry and Berg 1999), it is reasonable to assume that high energy thresholds must be passed also by anadromous individuals to attain maturity. This means that salmon that mature as 1SW fish should have greater lipid deposits at the end of the first summer than those that stay immature for another year and attain maturity as 2SW salmon.

Cold seawater and poor feeding opportunities appear associated with low growth in sea water (Saunders et al. 1983; Scarnecchia et al. 1991; Friedland et al. 1993), with young age at maturity as the most probable consequence in anadromous Atlantic salmon (Nicieza and Brana 1993; B. Jonsson et al. 2003). This appears to contradict the hypothesis by Thorpe et al. (1998), since large fish usually have higher, not lower, energy density than smaller fish (N. Jonsson et al. 1997; N. Jonsson and B. Jonsson 2003). However, the reaction norm may be low growth and early maturity if fitness is higher for slow growers attaining maturity at a younger rather than an older age, and vice versa for fast growers.

In coho salmon, Beamish and Mahnken (2001) hypothesized that juveniles that fail to reach a critical size by the end of their first marine summer do not survive the following winter. Recently, Beamish et al. (2004) found evidence for positive correlation between survival and growth for coho salmon in the Strait of Georgia. If expected sea survival is low also for slow-growing Atlantic salmon, selection may favour the storing of reserve energy at the cost of somatic protein growth, increasing the possibility of maturation as 1SW fish. After summers with good growth, expected sea survival should consequently be higher, making it more advantageous to stay as immature for another year before attaining maturity. In support of this contention, the size of 2SW salmon in the River Imsa are similar for all years irrespective of the size of 1SW fish (N. Jonsson et al. 2003), lending support to the hypothesis that a minimum size is required to delay sexual maturation beyond sea-age-1 (Fig. 1). Furthermore, the energy density needed for successful spawning is probably smaller for small than large fish, as spawning costs are relatively larger in large than small fish (e.g., Dutil 1986; N. Jonsson et al. 1991*b*, 1997). This means that the energy density needed to initiate maturation may increase with fish size. Thus, there may be no direct link between annual growth rate and age at maturity, but there may be a link among growth rate, lipid storage, and maturation through an as yet unknown process. Berrigan and Charnov (1994) hypothesized that high temperature and high growth rate had opposite effects on sexual maturation in fishes, which may be linked to variation in lipid deposition as discussed above. To investigate this, we have a need for systematic studies of growth rate and energy content of life history types of salmon reared at different seawater temperatures.

Iteroparity

Atlantic salmon are iteroparous and repeat spawners contribute to the marine production of the populations. However, most adults spawn only once before dying. A survey of 17 Norwegian salmon rivers revealed among population variation in repeat spawning between 2% and 25%, with the highest percentages in rivers dominated by 1SW fish (Table 1). In the Shannon River, Ireland, Went (1964) found that by weight, 7.3% of the spawners had spawned before, and Mills (1989) assumed that 80% of these were females. In the UK, about 5% of the salmon entering rivers survive to spawn a second time (Shelton 1986; Mills 1989). From the River Tana flowing along the border between Norway and Finland, Erkinaro et al. (1997) reported an average of 17% repeat spawners, 10% in males and 31% in females. From

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the Magaguadavic River, Canada, Martin (1984) reported that repeat spawners composed 14% of the run, and Chadwick (1988) considered previous spawners to be important in mitigating the effects of variation in sea survival of Atlantic salmon from Canada. However, there may have been a decrease in repeat spawning in Canadian rivers during the last part of the 20th century (Saunders and Schom 1985). In general, the chance of repeat spawning decreases with increasing fish size and sea age at maturity (N. Jonsson et al. 1991*a*, 1998). Furthermore, adult 1SW fish tend to spawn again in the subsequent autumn, whereas salmon reproducing for the first time as multi-SW salmon tend to become biennial spawners. Spawning mortality is higher in males than in females (B. Jonsson et al. 1991). Consequently, repeat spawning is more common in females than males (Mills 1989; Erkinaro et al. 1997; Niemelae et al. 2000), and there may be higher tendency of iteroparity in northern (cold) than southern (warm) rivers (Table 1), as found in American shad (*Alosa sapidissima*) (Leggett and Carscadden 1978; Glebe and Leggett 1981). But in only a few cases, repeat spawners appear important contributors to the future stock (Chadwick 1987; Mills 1989).

Why do adult salmon often die at spawning? First, fishing intensity on returning salmon at sea and in rivers is often high especially during summer (Crozier and Kennedy 2001; Dempson et al. 2001). Although as many as 60%–80% of the first-time spawners may survive the actual spawning and return to sea, as found in a small Norwegian river (B. Jonsson et al. 1990, 1991), only 10% or less of these return to spawn a second time, and the mortality of previous spawners is reported to be even higher in UK (Shelton 1986; Mills 1989). Fishing mortality differs among populations, and exploitation rates from 10% to more than 90% have been reported; exploitation occurs both in rivers and at sea (Turner 1972; Shearer 1986; Hansen 1990). From Canada, marine exploitation rates were recently estimated for Newfoundland populations (Dempson et al. 2001). There, fishing mortality was higher for large (mean 74%) than for small (mean 45%) salmon. A similar size selection in marine salmon fisheries was found in Norway (N. Jonsson et al. 2003). This may be because small salmon return later in the season than larger fish (B. Jonsson et al. 1990; N. Jonsson et al. 1990); in Norway, many return when the salmon fishery is closed, and because the nets are size selective, more large fish are caught than small fish (N. Jonsson et al. 2003). From this, one may assume that fishing mortality on repeat spawners will be higher than that on first-time spawners because of increased body size during their second sea sojourn. In North Irish waters, on the other hand, size selection appears different, with higher exploitations rates on 1SW than on 2SW salmon (Crozier and Kennedy 1994), probably reflecting variable exploitation patterns in different countries.

Second, 1SW salmon tend to invest relatively less energy into reproduction than multi-SW fish. Grilse may invest 50% or less of their total energy, whereas large salmon may invest as much as 70% or more when they stay in the river for reproduction (N. Jonsson et al. 1997; N. Jonsson and B. Jonsson 2003). Furthermore, large salmon may acquire surplus energy at a lower rate relative to their body size than smaller fish, so they need more time to obtain enough energy to go through a new reproduction cycle (N. Jonsson et al. 1991*a*); subsequently, they meet a greater mortality risk (Dutil 1986; N. Jonsson et al. 1997; Berg et al. 1998).

Third, large salmon fight more violently, and the chance of being injured during spawning may be higher in multi-SW than in 1SW populations, particularly for males, which fight more intensely than females (Fleming 1996; Fleming et al. 1996). The result is that repeat spawning is higher in females than males (Mills 1989; B. Jonsson et al. 1990; Niemelä et al. 2000), and this correlates negatively with mean size of the adults in the river (N. Jonsson et al. 1997).

Fourth, energy consumption during the spawning migration increases with water temperature, and mortality may therefore be higher in warm, southern rivers than in cold, northern rivers, as demonstrated for American shad (Glebe and Leggett 1981).

This means that mortality, age at maturity, and growth are the main factors influencing salmon production at sea, and in most populations, only a small fraction returns to the river for repeated spawning, in common to what has been found in other iteroparous salmonids, such as cutthroat trout (*Oncorhynchus clarkii*), Dolly Varden charr (*Salvelinus malma*) (B. Jonsson et al. 1984), and anadromous brown trout (B. Jonsson and L'Abée-Lund 1993).

Trends in production

Population abundance appears to have decreased during recent years on both the east and west side of the North Atlantic, especially in populations spawning in southern rivers (Potter and Crozier 2000; Klemetsen et al. 2003). There are at least three reasons for this: decreased marine survival, growth rate, and sea age at maturity.

Mortality seems to have increased in many populations during recent years (Hansen and Quinn 1998), and estimations of marine mortality of the River Imsa salmon have revealed a significant increase during the 1980s and 1990s (Fig. 2*b*). Sea survival varied among years, but the variation was not cyclic. The best correlation was found between recapture rates every 7th year ($r^2 = 0.11$, $p > 0.05$) (N. Jonsson et al. 2003). In this river, mean survival from smolt to adult between 1981 and 1999 was 8.9%.

Increased proportion of 1SW fish in Norwegian rivers might be influenced by the banning of the drift net fishery along the Norwegian coast since 1989 (Jensen et al. 1999). However, as the drift nets caught relatively more 2SW than 1SW fish, but the proportion of 2SW fish has decreased and not increased during the period (N. Jonsson et al. 2003), the banning from 1989 onwards appears not to be an important reason for the observed change in sea age at maturity.

Mean adult body length and size increment at sea of 1SW salmon (N. Jonsson et al. 2003) decreased significantly between 1981 and 1999 in the River Imsa (Fig. 2*a*). Crozier and Kennedy (1999) found decreased growth rate of the North Irish River Bush salmon, produced from 1- but not 2-year-old smolts. Friedland et al. (1998, 2000) indicated that this decrease may be caused by a change in spring temperature, and N. Jonsson and B. Jonsson (2004) found significant correlation between the May NAOI of the smolt year and the total weight increment at sea for 1SW salmon. Friedland et al. (1998, 2000) also found positive correlation between size increment at sea and survival, indicating a linkage between

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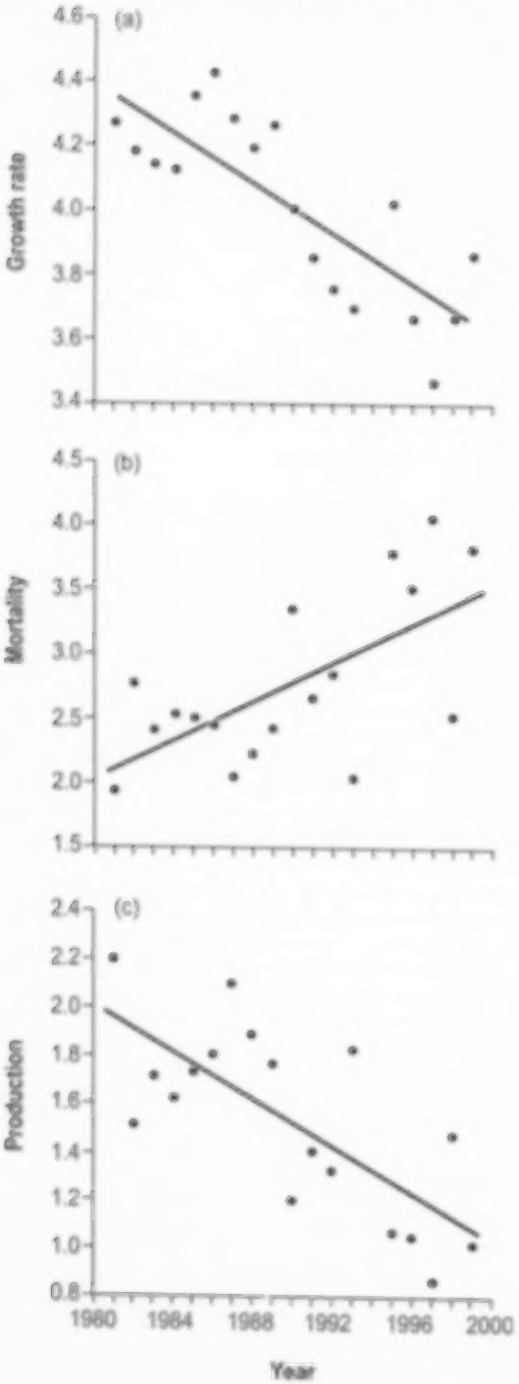

Fig. 2. Production variables of Atlantic salmon (*Salmo salar*) leaving the River Imsa as smolts between 1981 and 1999. (*a*) Mean marine growth (g_s = ln S_a – ln S_s; S_a is mass of adults, S_s is mass of the same fish as smolts) of each cohort. (*b*) Marine mortality (Z_s = ln N_s – ln N_a; N_a is number of returning adults each year, N_s is number of seaward-migrating smolts of the same cohorts). (*c*) Marine production (g_s/Z_s) of each cohort.

survival and growth. The most obvious environmental change during recent years has been the decrease in sea surface temperatures, which is largely governed by the strength of the Gulf Stream (Hansen and Quinn 1998). Low water temperature in the Northeast Atlantic is probably the reason for the low growth rate and small size of the 1SW fish and probably also linked to a decreased production of multi-SW salmon.

Marine production of Atlantic salmon appeared to decrease in the 1980s and 1990s because of increased mortality and decreased growth rate (Hansen and Quinn 1998). This is illustrated by the estimates of the marine production of the River Imsa salmon (Fig. 2*c*), which show a significant decrease during this period. In most years, the production is positive ($P_s > 1$, as defined in the Introduction), but the relationship between growth and survival showed negative production for the 1997 smolt cohort, meaning that the mass of the smolts was higher than that of the returning adults.

As the production decreased, sea age at maturity also decreased in many populations. Schaffer and Elson (1975) reported a tendency towards younger age at sexual maturity in North American rivers between the 1950s and 1970s. From the Northeast Atlantic, Gudjonsson et al. (1995) found decreased sea age at maturity in several Iceland stocks towards the end of the 20th century. The same seems to have occurred in the River Bush, Ireland (Hutchings and Jones 1998). In Norway, mean sea age at maturity appears also to have decreased gradually during recent years (Jensen et al. 1999; N. Jonsson et al. 2003). Progressively more Atlantic salmon attained maturity after one rather than two winters at sea.

Smaller, less fecund female salmon that bury their eggs less well in the gravel (Fleming 1996) may have reduced the production of smolts recruiting to the stock. There is some evidence that the smolt output from some rivers has decreased during the last decades, although trends are variable (Hutchings and Jones 1998; Scott 2001). In the River Bush, Ireland, smolt production declined strongly from 1975 to 1995, with an increase from 1996 onwards. In the Burrishoole, Ireland, the smolt output decreased between 1980 and 1991, but increased again after that. In the Girnock Burn and River North Esk, Scotland, there have been slight decreases since the 1960s. For the northeast Atlantic as a whole, there was a decreasing trend in most rivers between 1990 and 1995, but no trend between 1995 and 1999 (Scott 2001).

Reasons for variation in smolt output may be several, including variation in water quality and temperature (Scott 2001; Arkoosh and Collier 2002). The acidification of north European rivers has become less severe recently, and this, together with ongoing liming of the water in a number of salmon rivers, may have stabilized or slight improved the river production of smolts in northern Europe (Hesthagen and Larsen 2003).

In northern Europe, river temperature has increased recently because of climate change (Hoerling et al. 2001; Benestad 2002). This might result in improved survival as well as faster growth rate and more, younger, and smaller smolts (Økland et al. 1993). Correspondingly, mean smolt size in the Girnock Burn was smaller in the late 1990s than in the early 1980s (Scott 2001). If smolt size has decreased, the predation rate may have increased, since small fish are

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more vulnerable than larger ones (Lundqvist et al. 1994). Therefore, it is reasonable to investigate the variation in smolt size over time in more water courses to obtain a broader picture of the situation in the Atlantic. We have no similar information from southern populations of Atlantic salmon where the effect of climate change may be different.

The salmon fishery at sea is size selective, as the fish harvested along the Norwegian coast and in the fjords are larger than those that enter rivers (Dempson et al. 2001; N. Jonsson et al. 2003). For instance, 2SW salmon are exploited more heavily than 1SW fish during the return migration in coastal waters in Norway and Canada. However, the continued decrease in size of Norwegian salmon is probably not due to overfishing but to climate change. Fishing intensity has decreased in both east and west Atlantic, but fish size has still decreased (Klemetsen et al. 2003), indicating that factors other than marine fisheries are responsible for the decline.

Effects from salmon farming such as introgression of escaped fish in wild populations and the spread of parasites and contagious diseases, gyrodactylosis included (Heggberget et al. 1993; Bakke and Harris 1998), are negative to the production of wild Atlantic salmon (Hindar et al. 1991; Fleming et al. 2000; Youngson et al. 2001). However, escapement of farmed salmon appears not to be the explanation of the decrease in fish size or sea age at maturity recently observed (Gudjonsson et al. 1995; N. Jonsson et al. 2003). Introgression with farmed salmon should have increased, not decreased, growth rate and age at maturity of wild salmon (Fleming and Einum 1997; Fleming et al. 2000), because the hatchery stocks are selected for good growth and high sea age at maturity (Gjedrem et al. 1991; Gjerde et al. 1994). Escapement from fish farms, however, may have reduced the smolt production in rivers where cultured salmon spawn because of decreased reproductive success of the fish and ecological competition between the offspring of wild and farmed spawners (Einum and Fleming 1997; Fleming et al. 2000; Johnsson and Björnsson 2001). A suggested scenario is that escaped salmon from fish farms introgress the gene pools of wild fish. They disrupt local adaptations and reduce the genetic diversity of wild populations and thereby decrease the fitness of the fish and reduce the long-term production of Atlantic salmon in rivers (Hindar et al. 1991; Cross 2000; Youngson et al. 2001).

Earlier, overfishing may have been detrimental to salmon production. However, fishing efforts have been reduced both in high seas fisheries and home waters, especially during the last 15 years, decreasing the impact of overfishing, but little positive effect on wild populations has been observed (Klemetsen et al. 2003). There is an unknown effect of salmon caught as bycatch in other marine fisheries, and it is reason to investigate this more closely, as the bycatch problem may be greater than we presently perceive.

Research needs

The decreasing trends in growth, age at maturity, and survival have been established, but to understand and model the production of salmon at sea and use this in salmon management (Bisbal and McConnaha 1998), we need better knowledge about the key life history components: (*i*) the number of animals leaving fresh water, (*ii*) their growth at sea, (*iii*) marine mortality, and (*iv*) maturation schedules and their causes. What are the reaction norms between smolt age and (or) size and adult age and (or) size in various types of rivers and geographical area? Are young and small smolts attaining maturity at higher or lower sea age than older and larger smolts? Experiments testing effects of single factors in the laboratory and long-term population studies should be used to reveal trends and relationships.

The understanding of the relationship among water temperature, growth rate, growth efficiency, age at sexual maturity, and marine distribution of various populations is still poor. Furthermore, there is no information about optimal temperature for marine growth at different feeding rates, as there is for stream-living parr (Elliott and Hurley 1997; B. Jonsson et al. 2001). Is there a link between water temperature during early development and later performance (Rungruangsak-Torrissen et al. 1998, 1999; Angilletta et al. 2003)? Information on effects of water temperature on food consumption, metabolism, and growth has with success been used to model growth rate from water temperature in other species, such as brown trout, where it is used to forecast production (Elliott 1994). There is also a need for more knowledge about the relationship between growth efficiency and water temperature (B. Jonsson et al. 2001). Fish compete for food through exploitative competition, and competitors that extract energy more efficiently than others at a given temperature should be favoured (Wootton 1998). Thus, investigations of growth efficiency will help us to understand the competitive outcome of contests between species with similar food niches in the wild and the impact of climatic change on competitive ability of the fish.

The spatial distribution of salmon in the ocean should be studied (Friedland 1998). The environmental temperature cannot be judged unless the marine distribution through the year is known. Furthermore, we do not know to what extent the marine distribution changes with a change in climate and surface temperature in the sea or whether salmon sometimes are trapped in cold areas during winter from where they cannot escape. The marine distribution may also impact risk of predation, as potential predators may be more common in some than other areas.

There is little knowledge about marine predation, especially outside the estuary (Montevecchi et al. 2002). How much is taken by predators and to what extent is predation size selective? Furthermore, are parasites and contagious diseases important marine mortality factors? There has been speculation about the effect of sea lice, but almost nothing is known about how serious this parasite is for post-smolt survival and growth at sea (Bakke and Harris 1998).

The harvest of Atlantic salmon has been largely regulated through restrictions on equipment and time when fishing is allowed. But now, there is a move towards regulations through quotas based on forecast models (Wilzbach et al. 1998). Thus, there is a need for models where the links between climate and salmon production are better known than today (Potter et al. 2003). Furthermore, a part of the salmon is taken as bycatch in other fisheries. As yet, there is little knowledge about the extent of this bycatch and to what degree it impacts marine production of salmon.

Salmon farming is still increasing, and with that, increased negative impacts is possible on wild fish, at least in

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the short term, as documented in a number of studies (Hindar and Jonsson 1995; Fleming et al. 2000; Youngson et al. 2001). It is a challenge to retain viable wild salmon populations along side a large salmon-farming industry. Thus, there is a need for more knowledge about long-term effects of hatchery salmon on the productivity of wild conspecifics and competing species and how wild populations are best protected against negative impacts of farmed salmon. There is an urgent need for knowledge about how salmon farming can grow with minimum negative effects on natural ecosystems in general and wild salmon in particular (Gross 1998).

All in all, this research will improve the possibility to predict variation in salmon production at sea and help us interpret effects of climatic variation, fishing, and salmon farming, which many now consider to be the most serious threats against the production of Atlantic salmon at sea.

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Temporal synchrony and variation in abundance of Atlantic salmon (*Salmo salar*) in two subarctic Barents Sea rivers: influence of oceanic conditions[1]

Eero Niemelä, Jaakko Erkinaro, J. Brian Dempson, Markku Julkunen, Alexander Zubchenko, Sergei Prusov, Martin A. Svenning, Randi Ingvaldsen, Marianne Holm, and Esa Hassinen

Abstract: Long-term variation in Atlantic salmon (*Salmo salar*) stocks was analyzed in two Barents Sea rivers, the Teno and Näätämöjoki, that represent the northernmost distribution area of the species. In contrast to most of the North Atlantic area, these rivers are among a group of northern salmon rivers that, despite wide annual variation in catches, demonstrate no consistent trend for declining abundance. Variations in abundance were generally synchronous for the total catch and numbers of 1-sea-winter (1SW) and 2SW salmon during period of 1972–2003. Part of the variation observed in catches could be related to ocean climate conditions as the mean seawater temperature in July during the year of smoltification for the Kola section of the Barents Sea was significantly related to numbers of 1SW, 2SW, and 3SW salmon in the large River Teno. In contrast, NAO (North Atlantic Oscillation) indices were not related to salmon catches. The latest increase (1999–2001) in salmon catches in these rivers reflects both temporarily improved oceanic conditions and past management measures affecting offshore, coastal, and river fisheries.

Résumé : Nous avons analysé les variations à long terme des stocks du saumon atlantique (*Salmo salar*) dans deux rivières tributaires de la mer de Barents, la Teno et la Näätämöjoki, qui représentent l'aire de répartition la plus boréale de l'espèce. Contrairement à ce qui se passe dans la majeure partie de la région de l'Atlantique nord, ces rivières appartiennent à un groupe de cours d'eau qui, malgré d'importantes variations annuelles des prises, n'affichent pas de tendance soutenue de déclin d'abondance. Les variations d'abondance se manifestent généralement de façon simultanée dans les prises totales, les nombres de saumons ayant passé un hiver (1SW) et deux hivers (2SW) en mer durant la période de 1972–2003. Une partie de la variation observée dans les prises pourrait être reliée aux conditions climatiques de l'océan, puisque, les années de transformation en saumoneau, la température moyenne de l'eau de mer en juillet dans la section de Kola de la mer de Barents est significativement reliée aux nombres de saumons 1SW, 2SW et 3SW dans la grande rivière Teno. En revanche, il n'y a pas de relation entre les indices NAO (oscillation nord-atlantique) et les prises de saumons. La dernière augmentation des prises (1999–2001) de saumons dans ces rivières reflète à la fois une amélioration temporaire des conditions océaniques et les mesures d'aménagement du passé qui ont affecté les pêches au large, sur les côtes et dans les rivières.

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E. Niemelä,[2] J. Erkinaro, M. Julkunen, and E. Hassinen. Finnish Game and Fisheries Research Institute, Oulu Game and Fisheries Research, Tutkijantie 2, FIN-90570, Oulu, Finland.
J.B. Dempson. Fisheries and Oceans Canada, P.O. Box 5667, St. John's, NL, A1C 5X1, Canada.
A. Zubchenko and S. Prusov. Polar Research Institute of Marine Fisheries and Oceanography (PINRO), 6 Knipovich Street, Murmansk, Russia.
M.A. Svenning. Norwegian Institute for Nature Research, Department of Arctic Ecology, Polar Environmental Center, N-9296 Tromso, Norway.
R. Ingvaldsen and M. Holm. Institute of Marine Research, P.O. Box 1870, Nordnes, 5817 Bergen, Norway.

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[2]Corresponding author (e-mail: eero.niemela@rktl.fi).

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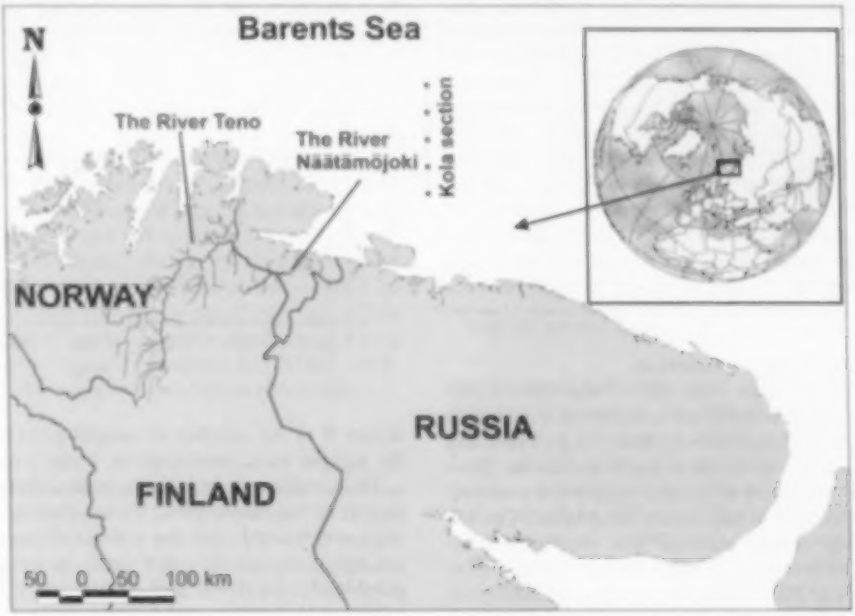
Fig. 1. Location of the Rivers Teno (70°N, 28°E) and Näätämöjoki (69°N, 29°E) and the general position of the Kola section sea temperature recording site situated in the Barents Sea.



Introduction

In many areas of the North Atlantic, populations of salmon (*Salmo salar*) either are in a state of decline or have already been extirpated (Parrish et al. 1998) such that concern over the continued survival of the species has been given more attention in recent years (Potter and Crozier 2000). Other stocks, while somewhat stable, have shown little or no improvement. In the past, high rates of exploitation in ocean fisheries were often associated with many stock declines and were seen as a serious threat to the future conservation of salmon (Mills 1993). Marine exploitation rates had been estimated in the range of 70%–90% on multi-sea-winter (MSW) components, whereas 1-sea-winter (1SW) stocks were commonly harvested at 40%–60% (e.g., Hansen 1988, 1990; Dempson et al. 2001). Yet, abundance of many stocks continues to fall despite the absence of, or great reduction in, directed marine salmon fisheries (Parrish et al. 1998; Friedland et al. 2003*a*; Dempson et al. 2004).

Specific reasons for the continued decline in abundance of salmon stocks are often not clear, but as stated by Parrish et al. (1998), multiple factors are likely responsible. To summarize, these factors typically result in reduced smolt output, increased marine mortality, and decreased sea age at maturity (Parrish et al. 1998; Jonsson et al. 2003). Thus, finding and studying salmon populations still considered generally "healthy", or those consistently achieving conservation spawning requirements, can often be problematic. Exceptions, however, include some salmon populations in northernmost Norway, Finland, and Russia that are not necessarily following the general decline observed in other Atlantic salmon stocks, but seem to fluctuate in the absence of a consistent decreasing trend (Jensen et al. 1999; ICES 2002).

With the potential for increased exploitation of the northern salmon stocks, impacts resulting from the proposed expansion of salmonid aquaculture into these northern areas, and the uncertain consequences resulting from global climate change (e.g., Turrell and Shelton 1993; Bigg 2000; Drinkwater 2000), it is important to examine the dynamics of salmon in rivers that still support abundant salmon stocks. Consequently, in this paper we examine the synchrony and long-term trends in abundance of salmon in two stocks from a small geographic area in the northernmost range of the Atlantic salmon distribution area that flows into the Barents Sea, namely, the Rivers Teno and Näätämöjoki, in the context of whether these northern stocks co-vary and follow the general declining trend of many other North Atlantic salmon stocks. Hansen and Quinn (1998), and more recently Friedland et al. (2003*a*, 2003*b*), suggested that the environmental conditions during the first months following migration to sea are critical periods influencing the subsequent growth, survival, and by extension, the abundance of salmon. Because the inflow of warmer water masses in the southwest is of crucial importance for the climate of the Barents Sea, with climate alternating between warm and cold periods (Loeng et al. 1992; Ingvaldsen et al. 2003), we also analyze whether the crucial influence of spring environmental conditions on salmon abundance, as suggested by Friedland et al. (2003*a*), can be detected in the northern Barents Sea rivers, the Teno and Näätämöjoki.

Materials and methods

Study area

The subarctic Rivers Teno (Tana in Norwegian) (70°N, 28°E; catchment area 16 386 km^2) and Näätämöjoki (Neidenelva in Norwegian) (69°N, 29°E; catchment area

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2962 km^2), border rivers between Norway and Finland, empty into the Barents Sea in a small geographical area on the coast of northernmost Norway (Fig. 1). More than 1100 km of the River Teno system are accessible to salmon, including the main stem and more than 20 tributaries supporting distinct substocks (Elo et al. 1994). Extensive salmon fisheries occur in the River Teno with a variety of gear, including weirs, gill nets, drift nets, seines, and rods (Henriksen and Moen 1997; Erkinaro et al. 1999). Distribution of salmon in the River Näätämöjoki covers 220 km along the main stem and two major tributaries (Niemelä et al. 2001). Salmon stocks in the Rivers Teno and Näätämöjoki are conserved, maintained, and enhanced only by fishery regulations as stocking of reared fish is prohibited in these systems.

Catch data and abundance estimation

In the absence of absolute measures of the salmon run sizes, the salmon catch is considered to represent a surrogate of abundance as used in other investigations (e.g., Friedland et al. 2003*a*). There are no salmon catch quotas in these rivers, and therefore, numbers of salmon caught are assumed to reflect actual variations in population abundance. The total weight of yearly salmon catches was estimated from postal questionnaires sent to fishermen and by catches converted into numbers of fish using the sea-age distribution of yearly catch samples.

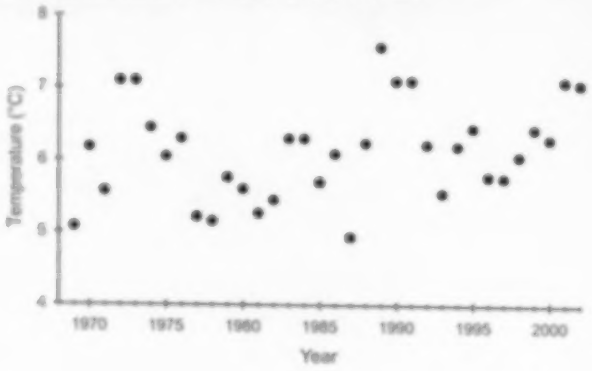
Scale samples of adult Atlantic salmon of the River Teno were collected by fishers using various gears throughout the fishing seasons of 1972–2003. Sampling took place in the middle section of the river covering 120 km within the area located between 70 and 190 km from the mouth (Fig. 1). In the River Näätämöjoki, rod and line, gill net, and seine were used to collect the scale material within the lowermost 60 km of the river throughout the fishing seasons of 1975–2003. Samples from the River Teno comprised 28 161, 7010, 10 179, 661, 22, and 2308 1SW, 2SW, 3SW, 4SW, and 5SW salmon and previous spawners, respectively. Samples from the River Näätämöjoki comprised 5508, 1734, 1360, 28, and 274 virgin 1SW, 2SW, 3SW, and 4SW salmon and previous spawners, respectively.

Statistical analyses

Co-variation in salmon stock abundance between the Rivers Teno and Näätämöjoki and linkages associated with Barents Sea temperature data was determined from Pearson correlation analyses based on the total declared catch of 1SW, 2SW, and 3SW salmon and all sea ages combined, as similarly carried out by McKinnell and Karlström (1999) examining co-variation in abundance of Baltic salmon stocks and in exploratory analyses of Friedland et al. (2003*a*) for North American stocks of salmon. However, correlation analyses are often confounded by problems associated with autocorrelation (Pyper and Peterman 1998). To account for autocorrelation in our analyses, we followed the approach outlined by Peterman et al. (1998) where corrected degrees of freedom ($N^* - 2$) are determined according to the following formula:

$$\frac{1}{N^*} = \frac{1}{N} + \frac{2}{N}\sum_{j}^{N/5} r_{xx}(j) r_{yy}(j)$$

Fig. 2. Mean sea temperature (°C) calculated from average values integrated vertically from 0 to 50 m across all stations of the Kola section for the month of July, 1969–2002.



where N is the number of sample pairs, $r_{xx}(j)$ and $r_{yy}(j)$ are the sample autocorrelations of x and y at lag j.

Temporal trends in salmon catches were examined and analyzed in two ways. First, scatter plots of abundance (catch) were constructed, and the estimated numbers of salmon by sea-age class, or the total catch in weight, was examined graphically by LOWESS regression (Trexler and Travis 1993), where each point in a series is predicted by a weighted combination of points around it in a regression equation (Wilkinson et al. 1986). Examination of LOWESS plots assisted in qualifying whether there were potential trends in the data. The optimal smoothing parameter selection was based on corrected Akaike's information criterion (AICc), and parameters were calculated by SAS PROC LOESS (SAS Institute Inc. 2001). Catches were then analyzed by autoregression-corrected regression analyses. Dependent variables included estimated total catch in the Rivers Teno and Näätämöjoki, estimated numbers of 1SW–4SW and previously spawned (PS) salmon in the River Teno catch, and 1SW–3SW and PS salmon in the River Näätämöjoki catch. Year was used as the independent variable. As virtually all linear regression models included autocorrelation in their error terms, the AR(1) error (autoregressive error at lag 1) structure was used. The validity of the AR(1) error structure model was compared with the ordinary least-squares regression model by likelihood ratio χ^2 tests. If the difference between models was not significant ($p > 0.05$), then the ordinary regression model was selected for the trend analysis. The analysis was performed by SAS PROC MIXED (SAS Institute Inc. 2001).

To examine co-variation between salmon abundance and ocean climate information, as explained above, we used the average sea temperatures in July at depths of 0–50 m, obtained from the Kola section in the Barents Sea (Tereshchenko 1996; S. Prusov, Polar Research Institute of Marine Fisheries and Oceanography, PINRO, unpublished data; Fig. 2). The Kola section is located along longitude 33°30′E in the central Barents Sea and intersects the Murman current from 70°30′N to 72°30′N (Fig. 1). The July temperature was selected to represent the conditions that young salmon from the northern rivers encounter when first entering the sea (cf. Friedland et al. 2003*b*). Temperature data were calculated from average values of every 5th metre

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integrated vertically from 0 to 50 m across all stations of the transect as described by Ottersen and Stenseth (2001) and Ozhigin et al. (2003). The Kola section is in close proximity to the rivers, and temperatures in the Kola section are significantly correlated with the temperatures in the central Barents Sea (Ingvaldsen et al. 2003), indicating that this section is representative for the variability of the Atlantic domain in the Barents Sea.

In addition to sea temperature, the NAO (North Atlantic Oscillation; Hurrell 1995) index was related to salmon catches. In this regression analysis, the independent variables were from the principal component adjusted Winter (December–March) NAO index during the first sea winter for each sea-age group and from the station-based NAO index in July during the first summer at sea (NAO Index Data were provided by the Climate Analysis Section, National Centre for Atmospheric Research, Boulder, CO 80307, USA, available from http://www.cgd.ucar.edu/~jhurrell/nao.html).

Results

The mean annual salmon catches from the Rivers Teno (1972–2003) and Näätämöjoki (1975–2003) were 139 tonnes (t; standard deviation (SD) = 48) and 9 t (SD = 3), respectively. In some years, more than 200 t of salmon have been caught in the River Teno, equivalent to a harvest of more than 60 000 fish (Fig. 3). Although the salmon run in the rivers was dominated by 1SW salmon (Table 1), MSW fish do make important contributions, for example, MSW fish comprise an average of 79% of the River Teno catch by weight.

Salmon abundance was positively correlated among the Rivers Teno and Näätämöjoki for 1SW ($r = 0.590$, $p = 0.010$) and 2SW ($r = 0.748$, $p = 0.010$) salmon and for the total catch (weight) where all sea ages are combined ($r = 0.663$, $p = 0.007$), suggesting simultaneous fluctuations in abundance of these northern stocks. However, 3SW salmon were not significantly correlated ($p = 0.095$).

Estimated salmon catches in the Rivers Teno and Näätämöjoki vary widely among years (Fig. 3). The lowest and highest figures show a threefold difference but no apparent trend for decreased abundance. However, numbers of 4SW salmon (River Teno) show a declining trend, but at the same time, there has been an increasing tendency for increased numbers of previous spawners in the River Teno catch (Table 2). In the River Näätämöjoki, the total salmon catch indicated an increasing trend over years (Table 2).

There were significant positive relationships between the mean sea temperatures in July in the year of smoltification and numbers of 1SW, 2SW, and 3SW salmon in the subsequent catches in the River Teno (Table 3). However, no such relationships were observed in the River Näätämöjoki. The adjusted winter and station-based NAO indices in the first July at sea after smolt run did not show relationships with the subsequent numbers of salmon in the catches.

Discussion

In contrast to observations of declining populations of salmon in many areas of the North Atlantic, stocks examined in this study from northern Norway and Finland have not shown any consistent decline in overall abundance. This is despite continued high rates of fishing that can approach 70% in rivers such as the Teno (Erkinaro et al. 1999), resulting in annual harvests of 20 000 – 60 000 salmon. The River Teno salmon catch has accounted for up to 15% of all riverine Atlantic salmon harvests in Europe (1995–2001) and as much as 22% in 2001 (ICES 2002).

Table 1. Sea age composition and corresponding proportion of males in Atlantic salmon (*Salmo salar*) samples from the Rivers Teno and Näätämöjoki (both emptying into the Barents Sea in northern Europe).

	River Teno		River Näätämöjoki	
Sea age	Sea age (%)	Males (%)	Sea age (%)	Males (%)
1	58	81	62	86
2	15	17	19	20
3	21	22	16	32
4	1	65	<1	75
5	<1	100		
PS	5	44	3	56
N	48 341	27 669	8904	5700

Note: PS, previous spawners; *N*, total number of samples.

Jensen et al. (1999) reported a significant increase in catch of 1SW fish in two Norwegian rivers, Repparfjordelva and Altaelva, in the close proximity to the River Teno, following the closure of the Norwegian drift-net fishery in 1989. Similar responses were noted in two Russian rivers in the Kola Peninsula since 1989 (Jensen et al. 1999). When a longer time period is examined, i.e., 1980–2002, the numbers of 1SW salmon in the catch of five northern Norwegian rivers have also increased significantly, in particular since 1989–1990. This is also attributed to the closure of the marine drift-net fishery (Ugedal et al. 2002). In the present study, high abundance of 1SW salmon has been observed since 1990, although the long-term trend is not significant when the entire period of 1973–2003 is considered. Notwithstanding the last 3 years of lower catches of 1SW salmon, the increase in the 1SW component during the 1990s could be due, in part, to a combined result of the closure of the Norwegian drift-net fishery (1989) and the increase in mesh sizes in the gill-net fisheries in the River Teno introduced in 1990.

Variability among salmon runs, as evidenced from catch (Rivers Teno and Näätämöjoki), is generally consistent between the rivers for 1SW and 2SW salmon and for the overall abundance when sea-age classes are combined in terms of weight, but not for 3SW salmon. The latter could be related to the overall lower contribution of 3SW salmon to the Näätämöjoki catch (~10%) compared with the Teno catch (~27% 3SW). Similar synchrony in catch fluctuations has been recorded between three other northern Norwegian rivers (Ugedal et al. 2002).

Previous investigations have established linkages between ocean climate signals and co-variation in survival or abundance of multiple salmon stocks (e.g., Friedland 1998; Friedland et al. 2003*b*). The synchrony or co-variation in abundance implies sharing or encountering similar environmental conditions at various life-history stages, although we note that different sea-age classes can be present in different areas owing to the length of time that fish remain at sea (Hansen and Quinn 1998). Consequently, knowledge of

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Fig. 3. Estimated yearly catches by weight (tonnes; all sea ages combined) or by numbers for 1-sea-winter (1SW), 2SW, 3SW, and 4SW salmon (*Salmo salar*) and previous spawners for Rivers Teno and Näätämöjoki. The solid line represents the LOWESS regression trend with individual smoothing values (*F*) shown separately for each component.

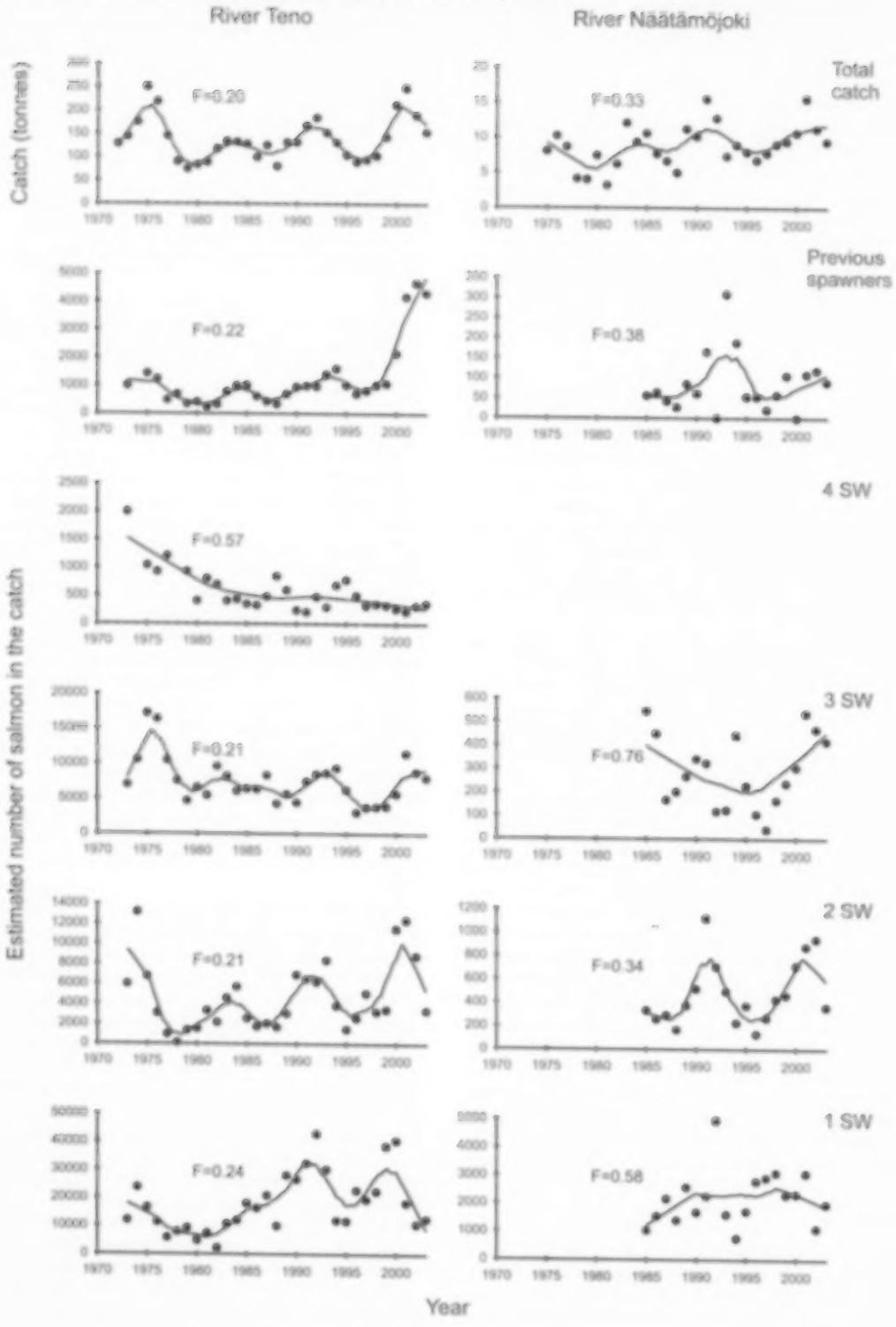

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Table 2. Results of trend analyses between the estimated numbers of salmon at different sea-age classes or total catch by weight (kg; all sea ages combined) versus year for Rivers Teno and Näätämöjoki.

River	Dependent variable	No. of years	Autoregression coefficient AR(1) of autoregression-corrected model	p value of likelihood ratio χ^2 test of the difference between AR(1)-corrected and ordinary linear regression model[a]	p value of the regression coefficient of year (significance of the trend of the selected model)	Direction of the trend
Teno	1SW	31	0.53	0.002^{AR}	0.163	
	2SW	31	0.52	0.002^{AR}	0.602	
	3SW	31	0.56	0.001^{AR}	0.322	
	4SW	29	0.65	0.005^{AR}	0.002	Declining
	Previous spawner	30	0.88	$<0.0001^{AR}$	0.046	Increasing
	Total catch (kg)	32	0.68	$<0.0001^{AR}$	0.703	
Näätämöjoki	1SW	19	0.02	0.944^{LR}	0.423	
	2SW	19	0.44	0.043^{AR}	0.387	
	3SW	19	0.52	0.026^{AR}	0.904	
	Previous spawner	19	–0.03	0.899^{LR}	0.759	
	Total catch (kg)	29	0.319	0.076^{LR}	0.026	Increasing

Note: Autoregression-corrected regression model or ordinary linear regression model was selected for trend analysis depending on the results of the likelihood ratio tests. Where statistically significant results for a year effect occurred, the direction of the trend was noted. SW, sea-winter.

[a]If the p value is <0.05, then the AR(1)-corrected regression was selected for valid model of the trend analysis (superscripted by AR), otherwise the ordinary regression model was selected (superscripted by LR).

Table 3. Co-variation between the mean July sea temperature from the Kola section of the Barents Sea and estimated numbers of salmon caught by sea-age class of Rivers Teno and Näätämöjoki.

River	Dependent variable	No. of years	AR(1) coefficient for autoregression-corrected model	p value of likelihood ratio χ^2 test of the difference between AR(1)-corrected and ordinary linear regression model[a]	p value of regression coefficient of temperature[b]
Teno	1SW	31	0.61	0.001^{AR}	0.023*
	2SW	31	0.5	0.004^{AR}	0.050*
	3SW	31	0.62	$<0.0001^{AR}$	0.002**
	4SW	29	0.89	$<0.0001^{AR}$	0.584
Näätämöjoki	1SW	19	0.03	0.901^{LR}	0.376
	2SW	19	0.42	0.104^{LR}	0.058
	3SW	19	0.5	0.030^{AR}	0.493

Note: Data were lagged according to the respective year salmon migrated out of the rivers as smolts and thus potentially influenced by spring marine environment conditions. Dependence of the salmon catch on temperature was analyzed by autoregression-corrected regression model or ordinary linear regression model depending on the results of the likelihood ratio tests. SW, sea-winter.

[a]If the p value is <0.05 then the AR(1)-corrected regression model was selected for regression model (superscripted by AR), otherwise ordinary regression model was selected for valid model (superscripted by LR) for numbers of salmon on temperature.

[b]Statistical significance of the dependence of salmon catch on temperature was indicated by asterisks: *, $p < 0.05$; **, $p < 0.01$.

salmon migration and distribution is fundamentally important. In the present study, no relationship with the NAO index and salmon stock fluctuation was detected, although the NAO index has been shown to influence the catches (Friedland et al. 2003*a*) and trends in sea age at maturity (Jonsson and Jonsson 2004) of Atlantic salmon in other investigations.

Precise knowledge of the location of specific feeding grounds of northern salmon populations, such as the Rivers Teno and Näätämöjoki, is still for the most part unknown, but it is believed to cover a large area of the Northeast Atlantic Ocean. Some data exist to substantiate this general belief. For example, salmon from the Kola Peninsula migrate to and feed at least as far away as the Faroe Islands as about 20% of salmon tagged north of Faroes were later recovered in the northern Russian area (Hansen and Jacobsen 2003).

Although accurate information on ocean migration patterns may be lacking, what is known is that northern European stocks of salmon leave rivers as smolt and enter the Barents Sea environment. In addition to noted fluctuations in salmon abundance, available information on sea temperatures from the Kola section also indicate considerable variation over years. For example, there was a rapid decrease in temperature towards the end of the 1970s, followed by a general increase overlaid by shorter-term variation. Earlier studies have demonstrated that the Kola temperatures show periodic fluctuations with periods of 3.3 and 7.3 years (Loeng et al. 1992; Ingvaldsen et al. 2003) and that the fluctuations are clearly linked to atmospheric forcing (Ådlandsvik and Loeng 1991). The climatic conditions affect the advection, growth rate, and distribution of zooplankton and fish larvae (e.g., Skjoldal et al. 1992; Giske et al. 1998), as well as fish population parameters such as growth, recruitment, migration, and distribution (e.g., Ottersen and Loeng 2000; Stenseth et al. 2002).

Other investigations of long-term climate variability in the Barents Sea have shown that the sea temperatures in 1990s were the warmest since the 1950s (Ingvaldsen et al. 2003).

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In parallel, smolt cohorts from the years 1998 and 1999 in the River Teno recruited historically high numbers of 1SW, 2SW, and 3SW salmon in the catches in 1999 and 2000, 2000 and 2001, and 2001 and 2002, respectively. These increases followed warmer sea temperature conditions during the years of smolt migration. However, although sea temperatures since 1999 have been above the long-term average, the number of 1SW fish has declined in three consecutive years since 2000. The reason for the decline in numbers of 1SW salmon could be related to lower smolt output followed by the low spawning escapements in the mid-1990s rather than to unfavorable temperatures at sea.

Following the increase in sea temperatures during the late 1990s, the numbers of PS salmon in the River Teno catches have also increased significantly. This is related to the higher numbers of 1SW fish in 1999–2000, as most of the PS salmon have spawned first as 1SW salmon and then spent a full year at sea before spawning a second time.

Fluctuations in the salmon abundance in relation to environmental conditions at sea should be taken into account when the effectiveness of the fisheries management regulations is assessed, as these fluctuations in the abundance can mask the effects of the regulatory measures. On the other hand, the relationships between stock variations and marine conditions may be obscured by the fact that the status of the stocks is poor and the environmental conditions may be impossible to discriminate from other factors, e.g., fishing. In the present study, these relationships could be analyzed for abundant salmon stocks with no overall declining trend. Fluctuations in catches can be quite severe and occur commonly over wide geographical areas (Dempson et al. 1998). Fluctuations can occur over a long periods of between 20 and 30 years (Bielak and Power 1986) or with shorter oscillating periods of between 8 and 9 years, such as in the rivers Teno and Näätämöjoki. Antonsson et al. (1996) found that the abundance of salmon stocks in northern Iceland demonstrated fluctuations similar to those found in the Kola Peninsula (Russia) 2–3 years earlier and hypothesized that stocks in other areas of the North Atlantic Ocean may show similar fluctuations in abundance with time differences based on the rate of movement of the ocean currents.

The northern salmon rivers are characterized by large natural fluctuations in both 1SW and MSW salmon stocks. This offers the possibility of examining further the potential influence of sea environmental conditions on salmon stocks with variable life histories. To date, the Rivers Teno and Näätämöjoki have been isolated from most human-induced impacts observed to affect negatively the production of salmon in many other populations (see Parrish et al. 1998) and hence confound attempts at establishing similar associations in those stocks. Thus, although many stocks of North Atlantic salmon continue to show declines in abundance (ICES 2002), particularly of the MSW component, the importance of maintaining and studying these largely pristine salmon stocks in northern Europe cannot be underestimated.

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Long-term changes in migration timing of adult Atlantic salmon (*Salmo salar*) at the southern edge of the species distribution[1]

Francis Juanes, Stephen Gephard, and Kenneth F. Beland

Abstract: The Connecticut River historically represented the southernmost extent of the North American range of Atlantic salmon (*Salmo salar*), but the native population was extirpated 200 years ago by dam construction. An extensive restoration effort has relied upon stock transfers from more northerly rivers, especially the Penobscot River (Maine). Recent work has shown differences in age structure between donor and derivative populations. Here we focus on a related life-history trait, the timing of the adult migration. We examined 23 years of migration timing data collected at two capture locations in the Connecticut River drainage. We found that both dates of first capture and median capture dates have shifted significantly earlier by about 0.5 days·year^{-1}. To conclude whether this is a consequence of local adaptation or a coast-wide effect, we also quantified changes in migration timing of more northerly stocks (in Maine and Canada). We found that the changes in migration timing were not unique to the Connecticut River stock and instead observed coherent patterns in the shift towards earlier peak migration dates across systems. These consistent shifts are correlated with long-term changes in temperature and flow and may represent a response to global climate change.

Résumé : Dans le passé, le fleuve Connecticut représentait l'extension la plus australe de la répartition du saumon atlantique (*Salmo salar*) en Amérique du Nord, mais la population indigène a été éliminée il y a 200 ans par la construction de barrages. L'effort important de réintroduction a été basé sur des transferts de stocks à partir de rivières plus boréales, particulièrement de la Penobscot (Maine). Des études récentes ont révélé des différences dans les structures d'âge entre la population d'origine et la population dérivée. Nous abordons ici une autre caractéristique démographique apparentée, le moment de la migration des adultes. Nous avons étudié des données sur la phénologie de la migration récoltées sur une période de 23 ans à deux points de capture dans le bassin versant du fleuve Connecticut. Les dates des premières captures et des captures médianes ont avancé significativement d'environ 0,5 jour·année^{-1}. Avant de décider s'il s'agit des conséquences d'une adaptation locale ou d'un effet répandu sur toute la côte, nous avons aussi analysé les changements de phénologie de la migration des stocks plus nordiques (au Maine et au Canada). Les changements de phénologie de la migration ne sont pas restreints au stock du fleuve Connecticut; il existe des patterns cohérents de déplacement des pics de migration vers des dates plus hâtives dans tous les systèmes. Ces déplacements coordonnés de dates sont corrélés à des changements à long terme de température et de débit; ils peuvent représenter une réaction au changement climatique global.

[Traduit par la Rédaction]

Introduction

Native populations of Atlantic salmon (*Salmo salar*) were extirpated from the Connecticut River 200 years ago as a consequence of dam construction. An extensive restoration effort has continued for almost 35 years based on fish originating from other rivers (Moffitt et al. 1982; Rideout and Stolte 1988). The majority (>90%) of imported fish released into the Connecticut originated from the Penobscot River, Maine (400 km northeast of the Connecticut River). Since 1995, all eggs for the program have come from adults that have returned to the Connecticut or their progeny. Recent work has shown that the age of maturity of returning adults differs between Connecticut and Penobscot River salmon

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F. Juanes.[2] Department of Natural Resources Conservation, University of Massachusetts, Amherst, MA 01003, USA.
S. Gephard. Connecticut Department of Environmental Protection, Inland Fisheries Division, P.O. Box 719, Old Lyme, CT 06371, USA.
K.F. Beland. Maine Atlantic Salmon Commission, 650 State Street, Bangor, ME 04401, USA.

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[2]Corresponding author (e-mail: juanes@forwild.umass.edu).

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(Martinez et al. 2001). Life-history traits such as the age at maturity and migration timing show population-specific variation heavily influenced by environmental and latitudinal effects in many anadromous fish species (Leggett and Whitney 1972; Taylor 1991; Quinn and Adams 1996). Long-term variations in return timing are generally thought to be phenotypic responses to changed local flow and temperature regimes (Hodgson and Quinn 2002; Lilja and Romakkaniemi 2003). The Connecticut River historically represented the southern edge of the range of the North American distribution of Atlantic salmon (MacCrimmon and Gots 1979). Given that both salt and fresh waters of the Connecticut River system warm earlier in the year than do those of the Penobscot River system and that historical reports suggest that the native Connecticut River salmon returned from the sea earlier than did the native Penobscot River salmon (Nordquist 1924; Baum 1997), we expected that the return date of Penobscot River salmon transplanted to the Connecticut River would gradually become earlier to avoid the warmer temperatures. Here, we examine whether the timing of return migration of adults to the Connecticut River has changed over the last 23 years for which data are available. To determine whether any observed changes are unique to the Connecticut River (and thus likely an early indication of local adaptation, see Taylor (1991)), we also analyze similar long-term datasets for other salmon stocks along the North American range of the species. Understanding the causes of trends in the timing of migrations can assist managers in evaluating the pace of stock development and determining if the program to restore Atlantic salmon at the southern edge of its range is at risk owing to climate change.

Methods

Connecticut River salmon datasets

Returning adult Atlantic salmon are captured at four dams: the Holyoke Dam on the Connecticut River (Holyoke, Massachusetts), the Rainbow Dam on the Farmington River (Windsor, Connecticut), the Design Specialties International (DSI) Dam on the Westfield River (Westfield, Massachusetts), and the Leesville Dam on the Salmon River (East Haddam, Connecticut). The Holyoke Dam is the first barrier to anadromous fishes on the Connecticut River. The other streams are tributaries that enter the Connecticut River downstream of the Holyoke Dam. All of the dams have fishways and salmon traps. Only salmon from the Holyoke Dam and Rainbow Dam fishways were considered in our analysis as adult returns to the other locations are either relatively recent and (or) very small in number. Atlantic salmon sea-returns are generated by stocking hatchery-reared smolts or hatchery-hatched fry generally upstream of these dams. No suitable salmon spawning habitat exists downstream of these two dams.

No adult salmon can get past these two dams without ascending the fishways, and we believe that very few salmon have ever passed up these fishways undetected. Both fishways are opened in early April, several weeks before the first salmon have been captured. The Holyoke fishway (10 m high, river km 139) is a fish elevator; Atlantic salmon are counted as they swim past a viewing window and are diverted into a trap. Data are collected from the salmon before either sending them to a cultural facility for breeding or releasing them back into the fishway to resume the upstream migration. Every 10th fish was released back into the river, the rest were retained as broodstock. The Rainbow fishway (18 m high, river km 104) is a vertical slot fishway with a counting house and viewing window near the halfway point in the fishway. All salmon captured at Rainbow are retained for breeding, and data are collected at the culture facility to which they are taken. All capture data from salmon at Holyoke and Rainbow are entered into a database managed by the Connecticut River Atlantic Salmon Commission. We obtained our data from this database. The Holyoke and Rainbow data formats were the number of salmon trapped by date at each dam from 1978 to 2000.

Salmon datasets from other rivers

The Penobscot River (Maine) dataset was collected at the Veazie Dam fishway, located near the head of tidal waters, from 1978–2001 (Fig. 1). Data were collected from migrating salmon in the trap located at the top of the fishway before either sending them to a cultural facility for breeding or releasing them back into the river to resume the upstream migration. The data format was the number of salmon trapped by date. Two datasets from Canadian waters were also available. The Millbank dataset was collected at the Millbank trap near the mouth of the Miramichi River, New Brunswick (Fig. 1). The number of salmon trapped was enumerated by day from 1953 to 1992 (Claytor 1996). The data were separated into small (<63 cm) and large (≥63 cm) salmon. The Torrent River dataset was collected on a daily basis from counts made at a fishway on the Torrent River in northwestern Newfoundland (Fig. 1). This dataset was scanned from a figure in Mullins and Caines (2000). Run timing data were presented as the date that 25th, 50th, and 75th percentiles of cumulative counts occurred by year from 1966 to 1999. Similar to the Millbank dataset, salmon were separated into small and large fish. Here, small returning fish were primarily 1SW (1 winter at sea or "grilse") in age (average of 97.5% (0.88 standard error, SE) 1SW between 1971 and 2000; see Mullins and Caines (2000)).

Analysis

The format of US datasets allowed us to calculate the date of first arrival, the median date of arrival (when 50% of the cumulative number of migrating fish were collected at the dam), and 5% and 95% percentiles (when 5% and 95% of the fish had reached the dam). All dates were converted to Julian dates for analysis. We used simple regression to test for decreases in the timing ("first" and "peak" of the run across years). We also regressed the days when 5% and 95% of the run occurred on each year as a measure of the overall temporal distribution of the migration. In addition, because we had individual-level data, we regressed the arrival date of each fish vs. year to estimate whether the average return date had changed during the study period.

For the Millbank data set, we also calculated the date of peak migration (i.e., 50% of the run), as well as the 5th and 95th percentiles for both small and large salmon. For the Torrent River, only 50th, 25th, and 75th percentiles were available. For both these systems, we also used simple re-

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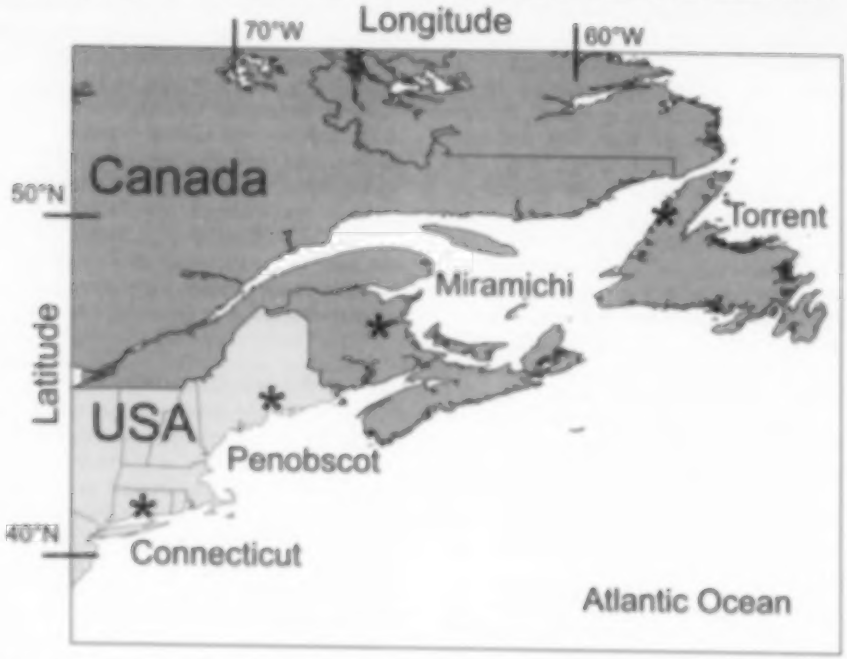
Fig. 1. Geographic locations (along the east coast of North America) of salmon (*Salmo salar*) runs studied here.



gression to assess trends in the migration timing for each percentile.

Environmental factors

We analyzed available data for long-term trends in water temperature and flow. We obtained median streamflow data (in cubic feet per second) by year for two US Geological Survey (USGS) stream gages: station No. 01184000 on the Connecticut River at Thompsonville, Connecticut, and station No. 01034500 on the Penobscot River at West Enfield, Maine. These two gages have the longest periods of record and large drainage areas compared with other stream gages on the same rivers (see McCabe and Wolock 2002) and are close to the dam locations. We examined the long-term relationship in streamflow using simple regressions of average streamflow during the migration season across years. Temperature records from the Connecticut were obtained from data collected at the Thompsonville USGS gage on a monthly (and occasionally bimonthly) basis. We used linear regression to obtain a relationship between the average monthly temperature over the migration period (May–July) across years (1978–1999). For the Penobscot River, we obtained water temperature records collected manually when tending traps or with temperature loggers (1994 to present) daily at the Veazie dam from May through October of 1978–2001. These records were grouped in 3-year intervals (except for the first interval, which encompassed 1978–1981). We used an analysis of variance (ANOVA) to detect differences in mean daily temperature across intervals and regression to examine whether average temperature increased across intervals. We obtained flow data for Canadian rivers from the Environment Canada website (http://scitech.pyr.ec.gc.ca/waterweb/formnav.asp?lang = 0). For the Millbank site on the Miramichi, we used data from the gage at Blackville (station No. 01BO001), which is the largest gaged station on the Miramichi River and has the longest record. For the Torrent River, we used data from the Bristol's Pool gage (no. 02YC001), the gage with the longest record on the Torrent River. Discharge was measured in cubic metres per second. No long-term temperature records were available for the Canadian Rivers. For the Miramichi, however, a recent stochastic water temperature model has simulated long-term water temperatures for 1977 to 1999 from air temperature data collected from Catamaran Brook in the Miramichi River system (see Caissie et al. 2001). We also assessed the influence of seawater temperature by summarizing sea surface temperature (SST) data for the areas closest to each river mouth. A 1° × 1° dataset (SST1) was available back to 1982, and a 2° × 2° dataset (SST2) was available back to the 1950s (downloaded from http://dss.ucar.edu/datasets/ ds277.0/; see Reynolds et al. (2002) for details on how datasets were interpolated).

To assess potential importance of environmental factors on changes in return timing, we correlated dates of peak migration against seasonal average temperatures, discharge rates, and SSTs obtained as described above. We also assessed whether similar trends in peak timing and environmental factors were due to similar trends over time (i.e., a statistical correlation) but had no underlying relationship by correlating the residuals (and SST anomalies). In almost all cases, the residual analyses showed similar results to those using the raw data and are therefore not shown here.

Results

Return timing

Changes in return timing towards earlier dates were detected for fish returning to the Connecticut River drainage.

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Table 1. Summary of return timing data and results of regression analyses of selected timing metrics against year.

Location	Collection site	Fish size	Timing metric	Years	Migration period	Time step	*N*	Mean	Slope	r^2	*p*
Torrent River	Fishway	Large	50%	1967–1999	June–Sept.	Daily	32	207	–0.9113	0.3472	0.0004
		Large	25%					195	–0.8142	0.2003	0.0102
		Large	75%					215	–0.8405	0.2563	0.0031
		Small	50%	1966–1999			33	208	–0.5133	0.2863	0.0013
		Small	25%					200	–0.4695	0.3071	0.0008
		Small	75%					218	–0.6856	0.3631	0.0002
Miramichi River	Millbank trap	Large	First	1954–1992	May–Nov.	Daily	39	139	0.0706	0.0125	0.4983
		Large	50%					227	–2.1265	0.5197	0.0001
		Large	5%					171	–1.9429	0.6008	0.0001
		Large	95%					271	–0.2858	0.0398	0.2236
		Small	First	1953–1992			40	153	–0.2998	0.1130	0.0339
		Small	50%					215	–1.8993	0.5969	0.0001
		Small	5%					174	–0.3958	0.4577	0.0001
		Small	95%					263	–0.6631	0.2360	0.0015
Penobscot River	Veazie dam	All	First	1978–2001	May–Nov.	Daily	24	136	–0.7309	0.2123	0.0235
			Second					138	–0.6974	0.2144	0.0227
			50%					183	–0.7083	0.3059	0.0051
			5%					157	–0.4043	0.2393	0.0153
			95%					250	–2.8069	0.5474	<0.0001
			All data				46 323	192	–0.9667	0.1854	<0.0001
Farmington River	Rainbow dam	All	First	1978–2000	April–July	Daily	23	123	–0.8379	0.2444	0.0165
			50%					149	–0.4456	0.1637	0.0555
			5%					127	–0.8755	0.3388	0.0036
			95%					166	–0.6788	0.2635	0.0122
			All data				842	148	–0.4374	0.0435	<0.0001
Connecticut River	Holyoke dam	All	First	1978–2000	April–July	Daily	23	130	–0.5444	0.1466	0.0713
			50%					152	–0.4951	0.1894	0.038
			5%					137	–0.5385	0.1840	0.0411
			95%					170	–0.5336	0.1741	0.0476
			All data				3 410	151	–0.0368	0.0003	0.2917

Note: Fish size refers to individuals <63 cm (small) and those ≥63 cm (large); timing metric is the cumulative number of migrating fish collected at each site, i.e., 50% is the median date of arrival, 5% and 95% represent when 5% and 95% of the fish had reached the dam; years is the time period over which the data were collected; N is sample size in years; mean is the average date for that metric in Julian days; r^2 is coefficient of determination; and *p* is probability.

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Fig. 2. Return timing (by day) vs. year for salmon (*Salmo salar*) collected at five sites on four rivers: (*a*) the Rainbow dam on the Farmington River, a tributary of the Connecticut River; (*b*) the Holyoke dam on the Connecticut River; (*c*) the Veazie dam on the Penobscot River, Maine. For (*a*) to (*c*), solid symbols represent peak migration (50% of total annual return) dates; open symbols represent dates of first migration. The solid and broken lines represent regressions through the peak and first migration dates, respectively. Regression equations are also presented. (*d*) The Millbank trap in the Miramichi River, New Brunwick; (*e*) the Torrent River fishway, Newfoundland. For (*d*) and (*e*), the solid and broken lines represent the peak migration dates (50% of the total return) for large (≥63 cm) and small (<63 cm) salmon, respectively. Open symbols represent large salmon; solid symbols represent small salmon. Regression equations are also presented.

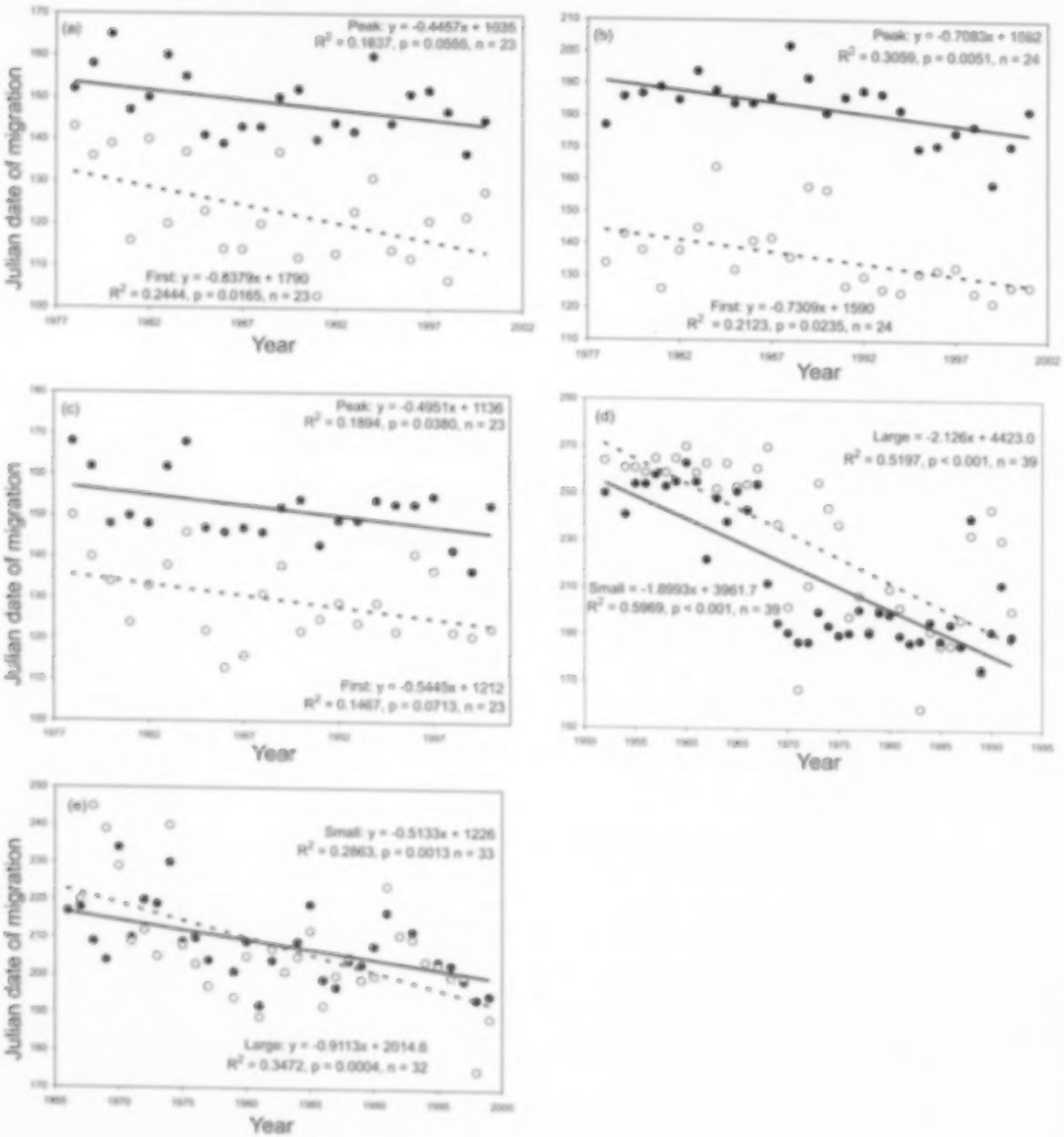

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Table 2. Long-term changes in abiotic factors (temperature and flow) in the Connecticut and Penobscot rivers.

Location	Factor	Data period	*N*	Slope	Intercept	r^2	*p*
Connecticut	Temperature	1978–1999	22	0.1300	−240.9	0.2607	0.0152
	Flow	1928–2000	73	61.7212	−109810.1	0.1893	0.0001
Penobscot	Temperature	1978–2002	8	0.2678	16.7746	0.8806	0.0005
	Flow	1902–2000	98	15.7695	−22769.7	0.0633	0.0120

Note: *N* is sample size in years; r^2 is coefficient of determination; *p* is probability.

Table 3. Correlations between dates of peak migration (50% of the run) and several environmental factors at five collection sites.

Collection site	Fish size	Environmental factor	N	*r*	*p*
Torrent River	Large	Flow	32	0.1660	0.3638
	Large	Temperature		nd	nd
	Large	SST1	18	0.6362	0.0045
	Large	SST2	32	0.3807	0.0316
Torrent River	Small	Flow	33	0.1959	0.2745
	Small	Temperature		nd	nd
	Small	SST1	18	0.6418	0.0041
	Small	SST2	33	0.1959	0.2745
Miramichi River	Large	Flow	32	0.0361	0.8444
	Large	Temperature	23	0.2220	0.3087
	Large	SST1	11	0.0965	0.7778
	Large	SST2	39	0.2261	0.1663
Miramichi River	Small	Flow	32	0.0152	0.9349
	Small	Temperature	23	0.0411	0.8521
	Small	SST1	11	0.4586	0.1560
	Small	SST2	40	0.0851	0.6013
Penobscot River	All	Flow	23	0.2286	0.2941
	All	Temperature	8	0.6291	0.0947
	All	SST1	20	0.3081	0.1862
	All	SST2	23	0.2465	0.2455
Rainbow dam	All	Flow	23	0.4876	0.0183
	All	Temperature	23	0.4110	0.0574
	All	SST1	20	0.4206	0.0648
	All	SST2	23	0.2273	0.2855
Holyoke dam	All	Flow	23	0.5290	0.0095
	All	Temperature	23	0.3076	0.1637
	All	SST1	20	0.3739	0.1044
	All	SST2	23	0.1473	0.4921

Note: Rainbow and Holyoke dams are both on the Connecticut River. Fish from Canadian systems (Torrent and Miramichi rivers) are separated into small (<63 cm) and large (≥63 cm) salmon. Temperature and sea surface temperature (SST) are measured in°C; flows are measured in cubic feet per second in US systems and in cubic metres per second in Canadian systems; SST1 refers to 1° × 1° SST data; SST2 refers to 2° × 2° SST data; *N* is sample size in years; *r* is correlation coefficient; *p* is probability; nd is no data.

At the Rainbow dam, this change was apparent whether we examined the date of first arrival or that of the 50th percentile or whether all data were used (Table 1; Fig. 2*a*). In contrast, for the Holyoke dam, we only detected significant negative relationships for the 50th, 5th, and 95th percentiles (Table 1; Fig. 2*b*). The rate of change of return timing varied between 0.4 and 0.9 days per year depending on metric and dataset used for a total of 9- to 21-day change over the 23-year time period.

Similar negative relationships were also detected for the other datasets. In the Penobscot, we also examined the arrival date of the second salmon because the trap was not always tended on a daily basis and in a few years the date of first arrival occurred when the trap was first tended. However, independent of the index used, all relationships were significantly negative with slopes ranging from 0.7 to 0.9 days per year, representing a change of 16–22 days (Table 1, Fig. 2*c*). For the Millbank dataset, all return timing metrics for both small and large fish showed a negative relationship except for the arrival of the first large fish and the 95th percentile for large fish. The slopes were generally larger and different among percentiles compared with other datasets (Table 1; Fig. 2*d*). Finally, the Torrent river returns also exhibited a significant negative change independent of percentile examined or whether small or large fish were used. The slopes varied between 0.5 and 0.9, indicating a 15- to 30-day change over the 33-year time period (Table 1; Fig. 2*e*).

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Environmental factors

Analysis of the temperature data showed significant increases in river temperature in both the lower Connecticut River and the Penobscot River (Table 2). Average flows also increased in both systems (Table 2). Correlations between environmental factors and dates of peak migration gave different results for different river systems (Table 3). For the Connecticut River, flow was significantly correlated with the change in peak migration timing for both Holyoke and Rainbow fish. River temperatures and SST1 were marginally nonsignificant for Rainbow fish. For the Penobscot and Miramichi (large and small fish) datasets, no significant correlations were detected with any of the environmental factors. For large fish in the Torrent River, both SST1 and SST2 were highly correlated with return timing changes, whereas only SST1 were correlated for small fish.

Discussion

We detected significant changes in the timing of migration to the Connecticut River drainage by Atlantic salmon over the last 23 years. These changes are reflected in the date of peak migration, as well as in other measures of timing of river ascent (e.g., 5%, 95%), and occurred at both locations examined. The estimated absolute change in migration timing varied from 9 to 21 days over that time period. We expected that owing to increased temperatures at lower latitudes, the adult migration to the Connecticut River would gradually become earlier compared with rivers in Maine, the main source of stocked salmon in the Connecticut before 1995 (Martinez et al. 2001), and more like historical populations and the populations in northern Spain, which are at a similar latitude and experience comparable temperature regimes (Nicieza et al. 1994; Kellogg 1999). Instead, we found that this earlier date of arrival (by about 30 days) into the Connecticut occurred immediately when the first salmon from Maine-origin stockings returned (compare intercepts in Figs. 2*a* and 2*b* with Fig. 2*c*). This rapid change suggests that migration timing was strongly influenced by local environmental factors.

Since the original stock transfer occurred, we observed similar rates of migration timing towards earlier dates in both the Connecticut and Penobscot populations, suggesting that both populations may be responding to similar environmental cues. Environmental and anthropogenic (including fishing and river obstacles such as dams and weirs) effects on Atlantic salmon run timing can be substantial (e.g., Lilja and Romakkaniemi 2003). Saunders (1981) speculated that because of extreme warming of the lower Connecticut and Long Island Sound, stocks with early entry would have the best chance of successful re-establishment. Earlier migrating adults in most populations are generally older (MSW) than later-arriving individuals, which are primarily 1SW fish (Jonsson et al. 1990; McKinnell et al. 1994; Klemetsen et al. 2003). Martinez et al. (2001) suggested that the very high and near lethal temperature experienced by later migrating adults coming into the Connecticut River would constrain them to earlier migrations and lead to the reduced number of (later-migrating) 1SW fish observed in this population compared with the Penobscot River. The Connecticut River stock has among the lowest levels of grilse of any European or North American population (see Hutchings and Jones 1998), averaging about 2% over the last 25 years (Friedland et al. 1996; Martinez et al. 2001). Friedland et al. (1996), in a study that incorporated fishing mortalities in estimating the fraction of each cohort that matured as 1SW, attributed the differences in age structure between the Connecticut and Penobscot River stocks to differences in rates of postsmolt growth during the summer. Interestingly, a re-analysis of the %1SW by year data presented in Martinez et al. (2001) and Friedland et al. (1996) suggests that the proportion of salmon maturing after 1SW is level (but with an increasing trend) for the Penobscot River but decreasing for the Connecticut River (p = 0.09 and 0.03 for the Martinez and Friedland data, respectively).

The changes in migration timing were not unique to the Connecticut and Penobscot River stocks but were also observed in other locations where data were available. Previous studies have suggested that factors such as fish size, sex, and rearing type (wild or hatchery-produced) can have substantial effects on migration timing of salmon (McKinnell et al. 1994). However, the consistency in the change in return timing across stocks, which likely differ in age and size structure, as well as in the proportion of hatchery-reared individuals, strongly suggests that all populations are being affected by similar environmental factors. Because of the previously established importance of temperature and flow rate in determining the relative timing of migration, we explored changes in discharge and temperature as potential drivers of the observed pattern in migration. Whether salmon respond to increasing or decreasing flow appears to depend on the stage of migration; increased flow can increase movement into a river from an estuary, whereas salmon migrating within the river may prefer decreasing flow (Trepanier et al. 1996; Erkinaro et al. 1999). Similarly the response to temperature is also variable and may depend on the magnitude and variability of the change (Trepanier et al. 1996). Our results show that temperature has been increasing along with average discharge rate over the last 25 years in both the Connecticut and Penobscot rivers. In fact, minimum and mean streamflow have generally increased in the eastern United States since 1970 (McCabe and Wolock 2002), and in New England, spring peak flow and center-of-volume runoff dates are trending to earlier dates over the last century (Hodgkins et al. 2003). Similarly, we detected increases in average temperatures during the migration period in both the Connecticut and Penobscot rivers, and in the Penobscot, peaks in temperature have been occurring earlier in the spawning period over the last 50 years (data not shown).

Changes in temperature and discharge rate along with variation in ocean conditions are all indices of climate change. Long-term analyses of the heat content and SST time series in the North Atlantic show statistically consistent warming over the last 30–50 years (Levitus et al. 2000; Barnett et al. 2001). Friedland (1998) has suggested that observed coherence patterns among different Atlantic salmon stocks are a reflection of broad-scale forcing functions, such as temperature, defining recruitment. For example, Friedland et al. (1993) observed a correlation between postsmolt survival and SST distribution in European salmon stocks. Fur-

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ther work has also shown that the abundance of 2SW spawners in North America is correlated to winter thermal habitat (Friedland 1998).

When we correlated the various environmental factors to the observed peak return timing dates, we found that long-term trends in seawater temperatures (SSTs) correlated strongly with changes in return timing in our northern system. In contrast, discharge rates were highly correlated with patterns in return timing in our southern populations (Connecticut River), whereas for those populations in the middle of the range, no significant correlations were detected. Changing SSTs and discharge rates are a consequence of global climate change (see above), but the differences we observed in the correlations are likely due to the migration pattern of the different populations. Homeward migrations are likely triggered by environmental cues, especially SSTs, experienced in the winter marine habitats near the Grand Banks (Friedland 1998). For northern populations such as the one migrating back to the Torrent River, ocean conditions close to the mouth of the river are likely correlated with those on the wintering grounds because of the short distance from these. In contrast, the Connecticut population is the most distant North American population from the overwinter habitats, and as such, the influence of winter SSTs may be masked more by local conditions by the time these fish arrive near the mouth of the Connecticut (Martinez et al. 2001). Populations at intermediate distances are likely affected by a combination of marine and freshwater cues (see Hansen et al. 1993). Regrettably, because of the limitations of the available environmental data for these populations, these ideas remain untested.

Pacific salmon (*Oncorhynchus* spp.) have also shown recent changes in return timing associated with environmental factors such as temperature and discharge. For example, variation in the migration timing among sockeye salmon (*Oncorhynchus nerka*) populations is primarily related to temperature (Hodgson and Quinn 2002), and the earlier upriver migration of sockeye in the Columbia River is correlated with long-term changes in temperature and river flow (Quinn and Adams 1996). Similarly, changes in the migration pattern of steelhead (*Oncorhynchus mykiss*) in the Columbia River are a reflection in part of changing temperature and flow regimes (Robards and Quinn 2002). In contrast, recent changes in run timing of Scottish populations of Atlantic salmon have been attributed to differential survival of early running (MSW) vs. late running (grilse) fish (Webb and Campbell 2000). This explanation is unlikely for the patterns observed here, as the changes in the grilse/MSW ratio are not consistent among rivers, being level in Canadian rivers, increasing in the Penobscot, and declining in the Connecticut (see above), and few of these populations are presently harvested.

Fishing can have an effect on return timing by changing the age/size structure of the population and (or) by targeting a particular component of the run. All recreational and commercial Atlantic salmon fisheries in the US have been banned (Kocik and Brown 2001; USASAC 2003) and therefore have had no influence on run timing to the Connecticut and Penobscot rivers. It is unclear whether existing recreational fisheries have the potential to affect the populations of the Torrent and Miramichi rivers, but it seems unlikely that the few remaining commercial salmon fisheries in Canada have the potential to affect any of the study rivers. However, a small-scale directed mix-stocked fishery for Atlantic salmon still exists in West Greenland (NASCO 2002). The impact of this fishery on the Canadian study rivers is unknown, but data indicate that very few fish from the Penobscot and Connecticut rivers are taken in this fishery (C. Legault, National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543, USA, personal communication). The effect of this fishery could have been more pronounced earlier in the restoration program before smaller quotas were adopted. Dempson et al. (2001) reviewed marine exploitation rates on Atlantic salmon in Canada and Europe over the last 20 years. They concluded that exploitation rates, particularly on the larger (MSW) salmon, were very high (on average 73% for Newfoundland stocks). Smaller (1SW) fish tend to experience lower exploitation rates likely as a combination of timing and gear selectivity. Even with fishing bans in place, numbers of returns have declined drastically in both the Connecticut and Penobscot rivers over the last decade (slope = –33.06, $r^2 = 0.67$, $p = 0.0022$ for the Connecticut; slope = –136.88, $r^2 = 0.63$, $p = 0.0033$ for the Penobscot; data from USASAC 2003), and many Newfoundland stocks have experienced substantial declines in abundance along with reduced marine survival rates (Dempson et al. 2001; Klemetsen et al. 2003). The particular causes of the decline and whether they can be attributed to in-river or at-sea portions of the life history remain unknown (USASAC 2003). However, our results suggest that the observed coast-wide changes in return timing over that same time period are an ecological response to climate change (see Walther et al. 2002) that may reveal a "fingerprint" (sensu Root et al. 2003) of environmental changes that are affecting the populations negatively.

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Phosphorus flux due to Atlantic salmon (*Salmo salar*) in an oligotrophic upland stream: effects of management and demography[1]

Keith H. Nislow, John D. Armstrong, and Simon McKelvey

Abstract: Little is known concerning the role of Atlantic salmon (*Salmo salar*) in the transport of nutrients to and from river systems. We used demographic data from the River Bran, an oligotrophic river in Scotland, UK, to construct a budget for the transport of phosphorus (P) and applied it to investigate the effects of management strategies and demographic rates on potential transport. At present, because few adults return to their spawning grounds, salmon export 0.2–0.5 kg P·year^{-1}. In contrast, increasing passage rates to a level sufficient to maintain a population without stocking would likely result in a gain of up to several kilograms per year. However, this effect depended on the retention of adult-derived P, which varies across systems and is poorly known at present. Egg-derived P exceeded that from adults at low (<25%) retention rates but was insufficient on its own to balance losses. Increased marine survival rates also increased the potential for positive P flux, while reduction in egg–smolt survival reduced the magnitude of transport. These results indicate the importance of considering within-river movements of individuals and nutrients and the need to fill critical data gaps in assessing the role of Atlantic salmon in nutrient transport.

Résumé : On connaît mal le rôle du saumon atlantique (*Salmo salar*) dans l'importation et l'exportation de nutriments dans les rivières. Des données démographiques dans la Bran, une rivière oligotrophe d'Écosse, nous ont servi à construire un bilan du transport du phosphore (P) que nous avons utilisé pour évaluer les effets des stratégies d'aménagement et des taux démographiques sur le transport potentiel. À l'heure actuelle, parce que peu de saumons retournent à leur site de fraye, les saumons exportent 0,2–0,5 kg P·an^{-1}. En revanche, l'augmentation des taux de passage à un niveau suffisant pour maintenir la population sans empoisonnement entrainerait vraisemblablement un gain pouvant atteindre plusieurs kilogrammes par année. Cependant, un tel effet suppose la rétention du P dérivé des adultes, un phénomène qui varie d'un système à l'autre et qui est actuellement mal connu. Le P dérivé des oeufs est plus important que celui dérivé des adultes aux taux faibles (<25 %) de rétention, mais ne suffit pas seul à compenser les pertes. Une augmentation des taux de survie en mer accroît la probabilité d'un flux positif de P, alors que la réduction de la survie de l'oeuf jusqu'au stade saumoneau diminue l'importance du transport. Nos résultats démontrent l'importance de tenir compte des déplacements des individus et des nutriments au sein du cours d'eau et soulignent la nécessité d'obtenir les données critiques manquantes nécessaires afin d'évaluer le rôle du saumon atlantique dans le transport des nutriments.

[Traduit par la Rédaction]

Introduction

Anadromous salmonids can be significant importers of marine-derived nutrients to temperate, upland stream systems and riparian forests and wildlife. Removing this source of nutrients, via barriers to upstream migration and fisheries exploitation, can reduce overall ecosystem productivity and diversity and threaten the sustainability of populations (Stockner et al. 2000; Stockner and Ashley 2003). The role of Pacific salmon (*Onchorhynchus* spp.) in nutrient dynamics and fish production in northwestern United States has been well documented and is an area of active research (Bilby et al. 1996; Wipfli et al. 2003). Several studies have shown increases in periphyton, invertebrate, and juvenile salmonid production (Chaloner et al. 2002; Chaloner and Wipfli 2002; Wipfli et al. 2003) in response to addition of salmon carcasses and higher production in streams with salmon spawning runs compared with streams without

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K.H. Nislow.[2] USDA Forest Service, Northeastern Research Station, 201 Holdsworth NRC; UMASS, Amherst, MA 01003, USA.
J.D. Armstrong. Fisheries Research Services Freshwater Laboratory, Faskally, Pitlochry, Perthshire PH16 5LB, UK.
S. McKelvey. Conon and Alness District Fishery Board, Aultgowrie Farm House, Aultgowrie, By Muir of Ord, Rosshire, IV6 7XA, UK.

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[2]Corresponding author (e-mail: knislow@fs.fed.us).

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salmon (Bilby et al. 1996; Cederholm et al. 2000). These results have led to explicit recommendations to managers, emphasizing the role of Pacific salmon as importers of marine-derived nutrients in maintaining ecosystem function and fisheries productivity (Bilby et al. 2001; Michaels 2003; Lackey 2003). In contrast with this large body of information on Pacific salmon, it is unclear whether anadromous Atlantic salmon (*Salmo salar*), their counterparts in the Atlantic basin, may function similarly as net importers of nutrients. Given major changes in the abundance and distribution of migratory Atlantic salmon (Parrish et al. 1998), understanding this role may be critical both for salmon conservation and management and for gaging the impacts of changes in population status and management strategies on river ecosystems.

Owing to key life history differences, it is unlikely that Atlantic salmon translocate nutrients to the same extent as Pacific salmon. Pacific salmon (with the exception of steelhead (*Onchorhynchus mykiss*)) are semelparous, with all individuals dying in rearing streams after spawning, whereas Atlantic salmon may migrate or wash out from spawning streams before dying downstream or leaving the river. In addition, the extended freshwater rearing period of Atlantic salmon results in fewer smolts (the life stage that migrates from fresh water to sea) and returning adults produced per unit area of rearing habitat compared with species such as pink salmon (*Onchorhynchus gorbuscha*) and chum salmon (*Onchorhynchus keta*) that migrate from rivers within a few months of emergence. However, under some circumstances, Atlantic salmon may have important impacts on nutrient fluxes. Survival of anadromous Atlantic salmon after spawning varies considerably among years and river systems, and many adults die and provide sources of marine-derived nutrients in some streams (Fleming 1998). However, there is almost no information on the extent to which Atlantic salmon carcasses are retained in rearing streams. Marine-derived nutrients may also be imported by routes other than carcasses. Spawned salmon eggs, which can compose 20% of the body weight of female spawners, are essentially all retained in rearing streams and might be a source of marine-derived nutrients even when spawners survive and outmigrate. Breakdown of muscle tissue for spawning and nest defense may also release marine-derived nutrients to streams (Jonsson et al. 1997). Previous studies on other species indicate that iteroparity and long freshwater rearing duration do not preclude a role for migratory fish in nutrient import. Durbin et al. (1979) found that the migration of the alewife (*Alosa pseudoharengus*), an iteroparous clupeid, resulted in a net import of marine-derived nitrogen (N) and phosphorus (P) and enhancement of plankton production in small spawning ponds in a coastal New England watershed. Schuldt and Hershey (1995) found that introduced chinook salmon (*Oncorhynchus tshawytscha*) resulted in a significant import of nutrients to a Lake Superior, US, stream in spite of extended freshwater rearing and small run size.

The importance of nutrient transport via salmon is not solely a function of total amounts transported. In systems that are characteristically low in nutrients (oligotrophic), relatively small chronic losses or gains can have major consequences. Many salmon streams, particularly in the uplands of larger river systems, are underlain by old, crystalline bedrock and are naturally poor in nutrients, with consequently low levels of primary productivity (Elliott et al. 1998). Compounding the intrinsically low productivity is a suite of anthropogenic influences that have acted to remove nutrients from upland systems, a phenomenon referred to as cultural oligotrophication (Stockner et al. 2000). Owing to their long history of intensive settlement (compared with Pacific basin systems), Atlantic salmon rivers may be particularly affected by cultural oligotrophication. As an example, in the New England region of the United States, >70% of the original forest (a major source of long-term nutrient storage; Foster 1992), practically all anadromous fish (a potential source of marine-derived nutrients), and most of the original population of the North American beaver (*Castor canadensis*) (whose activities store and make available large quantities of N and P; Cirmo and Driscoll 1993; Naiman et al. 1994) were lost from the northern forest ecosystem. More recently, acidification associated with atmospheric emissions has compounded losses of productivity (Driscoll et al. 2001). As this suite of anthropogenic effects (logging and land clearance, elimination of keystone species, and loss of stream buffering capacity) is common to salmon rivers to different degrees, loss of productivity may be of widespread concern.

Few studies have addressed nutrient transfer by Atlantic salmon. Lyle and Elliott (1998) presented a mass-balance assessment of several major salmon and sea trout rivers in the United Kingdom by estimating the flux of dissolved nutrients and salmonids (Atlantic salmon and sea trout) at the mouths of large rivers. They found that nutrients imported by adults exceeded nutrients exported by smolts, but that fish represented a very small fraction (<1%) of total nutrient flux through the system. However, the authors cautioned that nutrient export from the river mouth is likely to be dominated by anthropogenic sources (agricultural and municipal) on the mainstem that may not constitute important rearing or spawning habitat. They also suggest that transport by salmonids may be a much more significant component of fluxes to upland rearing streams. This suggestion was supported by a more recent mass-balance assessment of salmon nutrient transport in the River Imsa in Norway (Jonsson and Jonsson 2003). In this small (~1 km from the ocean) coastal river, as in the United Kingdom rivers studied by Lyle and Elliott (1998), migratory salmon accounted for a net import of nutrients to the river system. In the River Imsa, an oligotrophic river that largely consists of suitable spawning and rearing habitat, the proportion of total carbon (C), N, and P budgets accounted for by migratory salmon was generally an order of magnitude higher than that found by Lyle and Elliott (1998), encompassing as much as 17% of the total P budget in some years, in spite of low mortality and low carcass availability.

Assessing the role of Atlantic salmon in the nutrient dynamics of upland oligotrophic systems is of particular importance for fisheries and ecosystem management in the context of extensive human alteration of river environments. Relatively high gradient upland areas may provide the best physical spawning and rearing habitat for salmon. However, passage of salmon to and from these upland systems is impeded by the large in-river migration distance, during which mortality can occur, and a greater number of natural and artificial obstructions relative to lowland reaches. Atlantic

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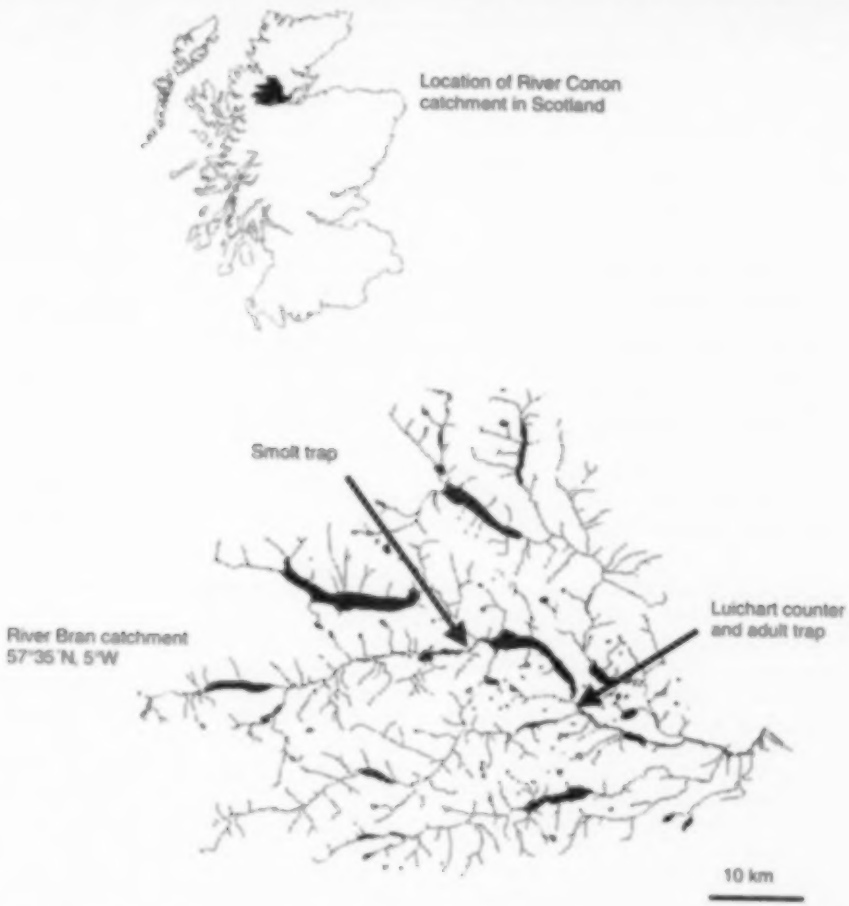
Fig. 1. Map of the River Bran system (Scotland, UK), showing locations of fish counter, fish passes, and smolt trap.


Location of River Conon catchment in Scotland
Smolt trap
River Bran catchment 57°35′N, 5°W
Luichart counter and adult trap
10 km

salmon are in decline throughout their range. In Scotland, the rate of decline is highest in those sectors of stocks within rivers that tend to return early in the year and spawn in upland areas. In Scotland, as well as in other regions (Parrish et al. 1998), populations impacted heavily by anthropogenic reductions in river connectivity and high marine mortality are supplemented or sustained by restoration and enhancement stocking of eggs and fry, resulting in a situation where considerable numbers of smolts are produced, but essentially no adults are able to access spawning areas. Understanding the potential effects of these management strategies on nutrient dynamics is critical for maintenance of productive, self-sustaining upland fisheries and ecosystems.

Our goal was to determine how variation in management strategies and population dynamics affect the role of Atlantic salmon in the transport of P. Phosphorus is the most frequently limiting nutrient in upland oligotrophic watersheds (Meyer and Likens 1979; Newbold et al. 1983; Bradford and Peters 1987), and several major field studies have demonstrated increased salmonid production in response to experimental P addition (Johnston et al. 1990; Deegan and Peterson 1992; Griswold et al. 2003). In anadromous species, P addition has resulted in decreased freshwater rearing times, larger outmigrant smolts, and higher smolt–adult survival rates (Slaney et al. 2003). For detailed study, we chose a Scottish upland system from which good data have been obtained on outputs of smolts, returns of adults, and the impact of obstructions to upstream migrations. The stock on the system is supported by a combination of enhancement stocking and natural spawning. Using these data, we compiled a P budget to assess the current P flux, explored the consequences of a number of management scenarios, and predicted the effects of variations in marine and in-river return migration mortality on Atlantic salmon. Though centered on a case study, our goal was to provide a framework for assessing salmon-associated nutrient transport applicable to a wide range of situations.

Materials and methods

The study site

The River Bran (57°35′N, 5°W) is a tributary of the River Conon in North Scotland, with a catchment of 191 km^2 (Mills 1964) (Fig. 1). Dissolved P on the Bran system is below the detection limit of 5 $\mu g \cdot L^{-1}$ (R. Harriman, Fisheries Research Services Freshwater Laboratory, Faskally, Pitlo-

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Table 1. Calculations and values for salmon transport of P budget in the River Bran.

Parameter	Equation	Values	Source
No. of stocked eggs		x = 629 000	River Bran stocking statistics
Mass per egg (g)		x = 0.058 g dry weight	Mills 1984
[P] eggs		0.002 841	Poston and Ketola 1989
Smolt number		x = 11 175	River Bran smolt trap
Mass per smolt (g)		x = 16 g	River Bran smolt trap
[P] smolts		0.0045 g wet weight	Lyle and Elliott 1998
No. of returning adults		x = 338.3	Fish counter on the Luichart Dam, supported by survival to returning fish of tagged smolts
No. of adults to spawning grounds	Returning adults × in-river passage proportion	In-river passage set at a range of rates from 0 to 1.0; current rate = 0.075	Current rate from Gowans et al. 2003
Mass per adult (g)		2500 g·adult^{-1}	River Bran adult trap
No. of carcasses	Adults × carcass retention via mortality	Carcass retention set at range of rates from 0 to 1.0	
Mass of carcasses (g)	(Mass·adult^{-1} × no. of carcasses) − mass of females as eggs	Proportion of females = 0.6	River Bran adult trap
$P_{carcass}$		Proportion of female mass as eggs = 0.2 0.0047 g wet weight	Mills 1984
Adult biomass (g)	Male biomass + female biomass		
P_{adults}	Adult biomass × P·g^{-1} adult	P·g^{-1} adult = 0.0047	Lyle and Elliott 1998
P_{eggs}	Proportion biomass as eggs × female biomass	P·g^{-1} egg = 0.002841	Poston and Ketola 1989
Net P	$(P_{adults} + P_{eggs}) - P_{smolts}$		

chrie, Perthshire PH16 5LB, UK, personal communication). As part of a plan to mitigate losses of salmon stocks associated with the generation of hydroelectricity, a salmon population has been established in the River Bran by stocking (1953–1970 and 1992–2002) progeny of fish from a neighboring tributary, the River Blackwater. Of an estimated wetted area of 0.661 km^2, an area of approximately 0.287 km^2 is stocked annually. The upstream passage of returning fish has been facilitated by a fish pass at the Conon Falls, which previously was a complete barrier. Fish moving to the headwaters negotiate a series of fish passes and lochs (Gowans et al. 2003).

A trap collected all adult salmon returning to the River Blackwater. The fish were then stripped, and the eggs were fertilized and held at the Contin hatchery. They were distributed widely throughout suitable rearing habitat in the River Bran, generally as eyed ova introduced into specially constructed artificial redds and occasionally as first-feeding fry. Fish leaving the system as smolts were collected each spring in a Wolf trap at Achanalt, examined, and then trucked and released downstream below Torachilty Dam. Stocking levels were increased over time, and the output of smolts from the River Bran reached a plateau level in 1998, suggesting that full productive capacity of the system had been reached. The stocking levels were determined from a combination of habitat surveys to identify total areas of suitable habitat and estimates of egg and fry densities needed to saturate the productive capacity (S. McKelvey, unpublished data). Current stocking levels are 3·m^{-2} and compromise between a target of 5·m^{-2} and maximizing the area stocked. Data collected from egg deposition and the resulting smolts and anadromous adults from 1995 to 2001 are considered in this study.

The total numbers of eggs and fry stocked were recorded. Smolts leaving the system were trapped throughout April–June and counted, and subsamples of 1000–2000 individuals were weighed and measured. Records from the resistivity counter, which used a wheatstone bridge circuit to detect differences in the conductivity of fish and water, in the Borland Lift fish pass at Luichart (Fig. 1) were taken as estimates of salmon returning to the system. A visual check in 1999 suggested that this counter is highly accurate, and counts tallied well with estimates of predicted returns based on the survival of a subsample of smolts tagged with passive integrated transponders and recorded automatically on their return migration (S. McKelvey, unpublished data). An estimate of the survival of salmon from Luichart to the spawning areas of the River Bran was taken from the radio-tracking observations of Gowans et al. (2003). Estimates of sex ratio and weights of adult fish were also taken from Gowans et al. (2003).

The P budget

A budget (Table 1) was constructed to estimate the net flux of P due to Atlantic salmon and to quantify the relative importance of constituent pathways under a range of scenarios. Estimates of P output (as smolts) and input were calculated from data collected in the River Bran in 1998–2000 along with parameter values obtained via previous studies.

Our basic budget equation is

$$\text{Net P} = (P_{adults} + P_{eggs}) - P_{smolts}$$

P_{adults} is the P concentration attributable to adults, adult size, return rate of adults, and retention within spawning streams; P_{smolts} is the P concentration attributable to smolt mass and number; and P_{eggs} is the P concentration attributable to egg number.

The annual P input from stocking was calculated as the product of the weight of stocked eggs and fry and their

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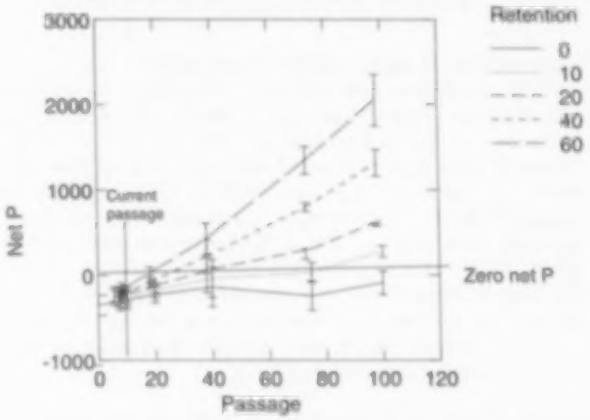
weight-specific P content (assuming no differences between eggs and fry before they have started to feed). The annual P input from returning adults was calculated in two components: the contribution from spawned eggs and from adults. Counts of returning fish at Luichart were adjusted to levels on the spawning grounds using a range (0%–100%) of passage (upstream survival) indices, which included the observed value (7.5%) under conditions pertaining in 1997 (Gowans et al. 2003). At each of the given passage levels, the total number of salmon was adjusted by the sex ratio to give the number of females. P input from their eggs was calculated as a product of the number of females, the fraction of their total biomass composed of eggs, and weight-specific P content of eggs. When female spawner passage was predicted by the budget to provide an equal or greater number of eggs as that from stocking, we no longer considered stocked eggs as an input term, simulating an end to stocking with sufficient spawner returns. Input from adults was calculated as the product of the remaining adult biomass (minus the eggs), the proportion of adult biomass retained (range from 0 to 0.6), and the weight-specific P content of adults.

We used this budget to predict net P flux from alternative management and demographic scenarios. Our basic scenario represents net P at current stocking, smolt production, and adult return levels over a range of passage and adult-derived annual P retention rates. Retention of adult P is a key parameter in the model and represents both P contributed from carcasses of dead spawners and P released by adult metabolism in nest defense and spawning activities. Adult-derived P retention rates ranged from 0 (no P retained) to a maximum of 60, which we felt was close to a maximum conceivable retention rate given outmigration, washout of carcasses, and advective transport of adult-derived particulate and dissolved P. In addition, this value of 60% approximates retention found by Lyle and Elliott (1998) and Jonsson and Jonsson (2003), making this level an appropriate maximum and a useful point of comparison among the three studies. In-river passage levels ranged from 0 (no upstream access; representative of highly regulated, impounded systems supported entirely by stocking) to 100% passage.

Outputs from the budget scenarios were used to assess the effects of changes in river passage, differences in adult P retention, and changes in marine and pre-smolt mortality on the magnitude and direction of P flux in the River Bran. Specifically, we considered the following questions: (*i*) What is the maximum P drain with effectively zero adult return? (*ii*) What is the net P flux under current conditions of in-river passage of returning adults? (*iii*) If upstream passage of fish can be improved to the point that natural spawning replaces stocking, will there be a net gain or drain of P to the system? (*iv*) What is the contribution of P from spawned eggs versus adults? (*v*) How will changes in egg–smolt and marine survival influence the P budget? Output was expressed as the median and range of values across the 3 years of data. We were particularly interested in the relationships of these variables to the threshold of zero net P flux, the point at which salmon become a net gain or drain on the system. To make this assessment, we determined whether the range of P flux for a given scenario was negative (range below and not overlapping the zero threshold), positive (range above and not overlapping the zero threshold), or zero (range overlapping the zero threshold).

Fig. 2. Relationship between adult passage and Net P flux ($g \cdot year^{-1}$) from 1998 to 2000; egg stocking, smolt outmigration, and adult return levels are at five different adult P retention levels. Adult passage is the percentage of adults returning to the lower River Bran that successfully access spawning grounds in the upper river. Points represent median values over the 3 data collection years; error bars indicate the range of values.



Results

P transport with low adult passage

Under conditions of zero adult return, as occurs in stocked systems above impassable barriers and has historically occurred in the River Bran, a loss of 316–553 g $P \cdot year^{-1}$ would result (Fig. 2). This deficit is the balance of 290–550 g P introduced as stocked eggs and 706–865 g P lost as smolts. Under current conditions of low (7.5%) passage (Gowans et al. 2003), Atlantic salmon result in a net drain on P from the River Bran (Fig. 2). P contained in outmigrating smolts exceeds that of adult and egg inputs under all scenarios. The magnitude of this loss depends on what proportion of salmon adult P is retained within the system, but this effect was relatively small, ranging from a loss of 284–502 g $P \cdot year^{-1}$ under zero adult P retention to a loss of 140–317 g $P \cdot year^{-1}$, with retention of 60% of adult P. At the upstream passage rates recorded in 1997, a drain of ~100 g $P \cdot year^{-1}$ would result even if all (100%) adult P was retained in the system.

P transport under increased rates of adult passage

Increased passage of adults to spawning grounds strongly influenced predicted net P flux. In contrast with the low-passage scenarios, resultant P fluxes at higher passage rates were greatly affected by differences in adult P retention (Fig. 2). For example, at 20% passage, P input could balance P outputs, but only at the highest level (60%) of adult P retention (Fig. 2). At 75% passage rates, budgets were balanced (zero net flux) at relatively low levels (10% retention rates) and resulted in net positive fluxes of >1 kg P with high (>20%) retention. Given current average sex ratio and fecundity in the River Bran (Table 1), meeting spawning targets for

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egg deposition would require between 187 and 354 adults returning to the spawning grounds, which corresponds to ~50% passage. These returns resulted in large between-year differences in net P flux (Fig. 3). In general, P losses by smolts were balanced by adult and egg contributions at 10%–20% adult P retention and were predicted to result in high net P imports of up to 2 kg P·year^{-1} at higher retention percentages (Fig. 3).

Contribution of eggs compared with adults

Budget predictions indicated that P associated with spawned eggs could be a major component of total P flux under some scenarios. At current low passage rates (7.5% of returning adults), P from eggs exceeded P from adults at all retention levels. At higher passage rates (>20%), P contribution of eggs exceeded P contributions of adults until retention levels exceeded 20% (Fig. 4), and at high retention and passage levels, adult contributions were two- to four-fold greater than egg P. Importantly, egg contributions alone were not sufficient to balance the P budget even at the highest levels of in-river passage (Fig. 2; zero retention line) under current smolt and marine survival rates.

Effects of changes in marine and freshwater survival

Changes in marine survival had strong effects on P flux via migratory salmon. Increasing survival from current levels of 2% of outmigrating smolts to 7%, which was historically exhibited by many salmon-rearing streams in eastern Scotland, greatly increased the import of P to the system. This high marine survival scenario resulted in a balanced P budget even at current low passage (7.5%), given a high (60%) retention rate (Fig. 5). Increasing passage rates to 75% of returning adults resulted in predicted positive net P flux with retention rates as low as 10% and net P imports of 2–4 kg at high retention levels (Fig. 5). Reducing marine survival to 0.5% resulted in negative P flux at all retention levels, even at high (75%) passage (Fig. 6).

Changes in egg–smolt survival also strongly affected P flux. In general, at current marine survival rates, reduced egg–smolt survival reduced the overall scope of both negative and positive potential transport, as fewer smolts were predicted to transport P from the system, yielding fewer adults to transport it back (Figs. 7 and 8). Reduction in egg–smolt survival from current levels of ~2% to 0.5% reduced the overall scope of P transport and resulted in small (<300 g), positive net P flux under current low passage at all retention levels. In contrast, doubling egg–smolt survival to 4% of deposited eggs strongly increases the scope of P transport, with potential losses (under low passage and retention scenarios) and potential gains (under high passage and retention scenarios) of >1 kg P·year^{-1}.

Discussion

Our analysis provides an effective framework for bracketing the conditions under which salmon may transport nutrients to and from rearing streams. This understanding is an essential element in moving towards an ecosystem-level approach to salmon research, conservation, and management (Naiman et al. 2002). We clearly map out the way in which aspects of Atlantic salmon life history interact to determine

Fig. 3. Relationship between adult P retention and Net P flux (g·year^{-1}) from 1998–2000; egg stocking, smolt outmigration, and adult return levels are at spawning target adult passage levels. Points represent median values over the 3 data collection years; error bars indicate the range of values.

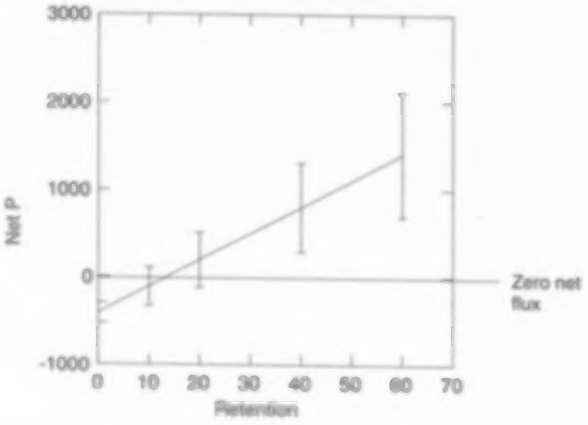
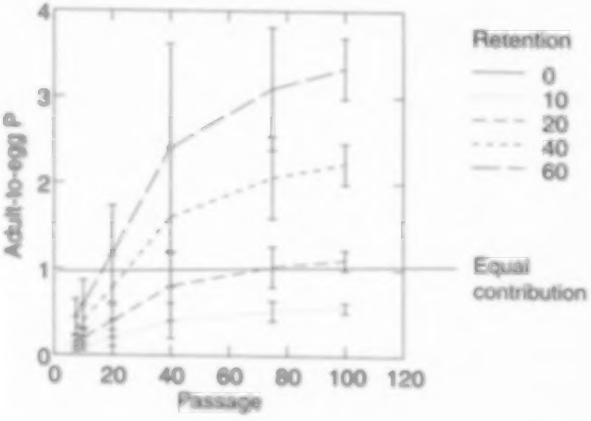


Fig. 4. Relationship between adult passage and the ratio of adult- to egg-derived P from 1998–2000; egg stocking, smolt outmigration, and adult return levels are at four different adult P retention levels. Adult passage is the percentage of adults returning to the lower River Bran that successfully access spawning grounds in the upper river. Points represent median values over the 3 data collection years; error bars indicate the range of values.



the magnitude and direction of nutrient flux. While this study is focused on specific conditions in the River Bran, our approach is amenable to modification and should be widely applicable to a range of systems and situations.

We found that under current conditions of smolt production, marine survival, and in-river passage, which have been relatively stable over the past several years, Atlantic salmon currently are a net drain on the P budget of the River Bran, with smolts consistently exporting more P than is predicted to be returned from eggs and adults. This is in contrast with the findings of both Lyle and Elliott (1998) and Jonsson and Jonsson (2003) of positive net import of nutrients via migratory Atlantic salmon. Our prediction of net export is robust

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Fig. 5. The effects of marine survival (proportion of outmigrating smolts returning to the river) on net P flux at four different adult P retention levels under the current passage level of 7.5%. Adult passage is the percentage of adults returning to the lower River Bran that successfully access spawning grounds in the upper river. Points represent median values over the 3 data collection years; error bars indicate the range of values.

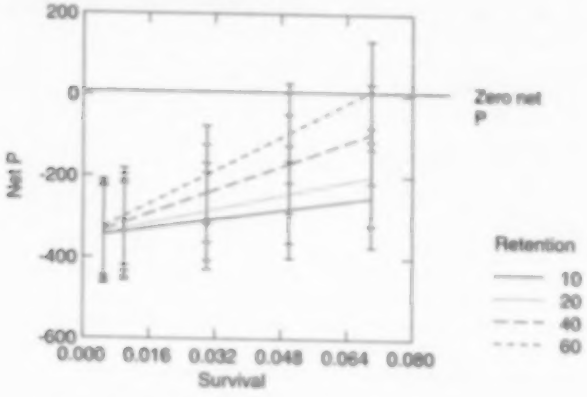


Fig. 6. Effect of marine survival (proportion of outmigrating smolts returning to the river) on net P flux at four different adult P retention levels under an increased passage level of 75%. Adult passage is the percentage of adults returning to the lower River Bran that successfully access spawning grounds in the upper river. Points represent median values over the 3 data collection years; error bars indicate the range of values.

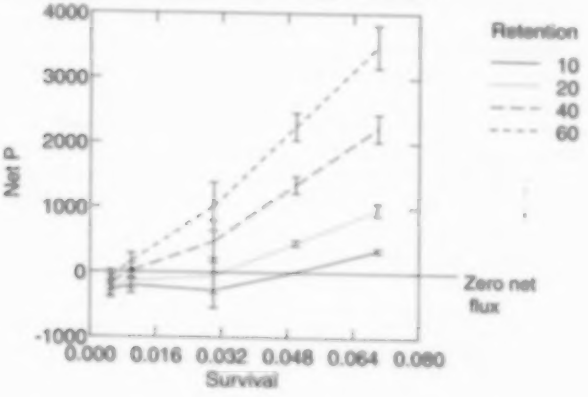


Fig. 7. Effect of smolt survival on net P flux at four different adult P retention levels under the current passage level of 7.5%. Adult passage is the percentage of adults returning to the lower River Bran that successfully access spawning grounds in the upper river. Points represent median values over the 3 data collection years; error bars indicate the range of values.

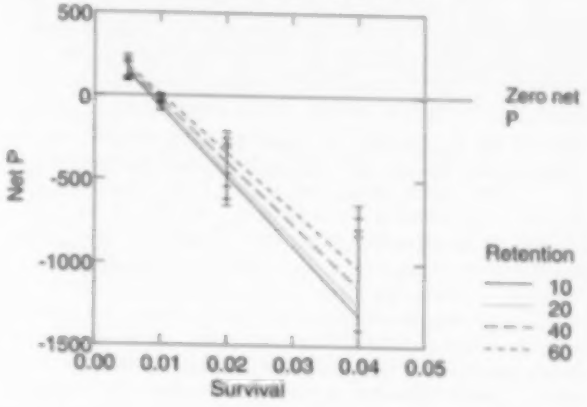
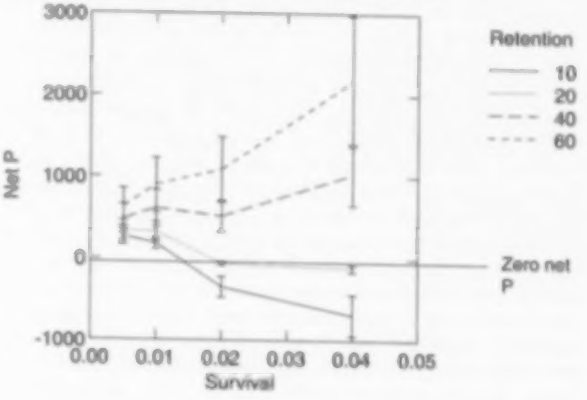


Fig. 8. Effect of smolt survival on net P flux at four different adult P retention levels under an increased passage level of 75%. Adult passage is the percentage of adults returning to the lower River Bran that successfully access spawning grounds in the upper river. Points represent median values over the 3 data collection years; error bars indicate the range of values.



to the major element of budget uncertainty, retention of adult P. As some studies have shown that overyearling salmon parr leave upstream spawning areas a year or more before smolt migration (Meister 1962; Riddell and Leggett 1981; McCormick et al. 1998), net export may be even greater than we predict. For example, in the Girnock Burn in northeastern Scotland, Youngson et al. (1994) found that up to 30% of overyearling parr moved downstream in the autumn.

Our analysis indicates that net loss of P via migratory salmon in the River Bran is primarily the result of constraints on the ability of adults to reach spawning grounds. Increasing access to spawning grounds (e.g., by increasing the effectiveness of bypass lifts on dams, a process that is currently underway on the River Bran) to the levels observed in rivers lacking barriers to passage (in which there is an approximately 81% survival to spawning; A. Gowans, Environment Agency, Ghyll Mount, Gillian Way, Penrith 40 Business Park, Penrith, Cumbria CA11 9BP, UK, personal communication) would likely result in at least a balanced P budget and quite probably a net gain of P to the system. The probability of net import is reinforced by our finding that adult passage at replacement levels (adequate to achieve spawning targets) produced positive P flux under most retention scenarios. Therefore, in conjunction with the two previous studies on wild populations (Lyle and Elliott 1998; Jonsson and Jonsson 2003), our results indicate that self-sustaining populations of migratory Atlantic salmon are net importers of marine-derived nutrients.

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Although we predict that improved passage will improve the P budget of the River Bran, retention of adult-derived P has had a very strong effect on the magnitude and direction of P flux. This sensitivity points to a major gap in our understanding of the role of Atlantic salmon in the transport of P to and from rearing areas. While marine-derived P from salmon eggs could equal or exceed adult-derived P under some conditions, it was not sufficient to counter current smolt losses, underscoring the need to accurately assess adult retention. In their analysis of P budgets across several English rivers, Lyle and Elliott (1998) found that on average 60% of the P contained in returning adult salmon was retained in the river system, largely because of in-river mortality of kelts (adult salmon after they have spawned). This high level of retention was an important factor in their finding of a net positive flux of marine-derived nutrients, including P, in their study rivers. However, this level of carcass P retention is almost certainly an overestimate of retention in upland spawning and rearing sections of river systems. Many kelts may not die until they are in the lower sections of rivers, and of those that do die in upstream rearing sections, many of their carcasses, as well as particulate and dissolved material derived from these carcasses, will be transported significant distances downstream of rearing areas. Previous studies on Pacific salmon have shown that retention of carcasses can be significantly influenced by the hydrologic regime and habitat structure of spawning reaches and that mechanisms of retention and movement are complex (Cederholm et al. 2000). In contrast, Jonsson and Jonsson (2003) found that in the River Imsa in-river mortality was low, and carcasses were a relatively minor source of adult-derived P. Instead, most adult-derived P was contributed by metabolic losses from the breakdown of body tissues while adults were on the spawning grounds. While these losses are somewhat straightforward to measure in a small coastal river such as the River Imsa, they are problematic in larger systems, where losses can occur before adults reach the spawning grounds, and processes such as advection can transport nutrients lost on the spawning grounds to lower river reaches. In strongly P-limited systems, however, dissolved P can be rapidly absorbed by benthic biofilms and taken up by streamside vegetation, providing a mechanism for local retention (Naiman et al. 2002). Studies in which outmigration, mortality, metabolism, and carcass retention of Atlantic salmon can be assessed at a finer spatial scale than has been accomplished previously are therefore critical in improving our ability to predict the role of salmon in nutrient dynamics.

At present, smolt and adult production on the River Bran is supported by stocking. We found that stocking strategy has an important influence on potential P flux in the system. Most importantly, continuing to stock and produce smolts from a system where adults lack access to spawning areas ensures a net loss of P from the system via migratory salmon. However, this P drain should be self-regulating to some extent. If smolt production is positively associated with P availability, then P loss should eventually result in lower smolt production and a smaller yearly loss of P from the system, so that overall salmon production and P flux should stabilize at some lower level. For the River Bran, our results indicate that this production "floor" may occur at an egg–smolt survival of ~1%, less than half of current values, representing a major loss of productive capacity.

As we do not have a full P budget for the River Bran, it is difficult to evaluate the importance of P flux via migratory Atlantic salmon relative to total P transport in this system. However, the River Bran is similar in some important respects to the River Imsa, where total P fluxes have been measured (Jonsson and Jonsson 2003). Both systems have similar P concentrations in streamwater (<5 $\mu g \cdot L^{-1}$) and similar overall fluxes of salmon-derived P (several kg) at "natural" passage and retention levels. While the River Bran is a considerably larger system in total, the salmon-rearing zone of the River Bran has a similar drainage area as that of the River Imsa. If these similarities translate to similar percentage transport, this finding provides support for a potentially significant role of salmon in oligotrophic river systems.

Determining the dynamics and thresholds involved in this process point to knowledge gaps that must be bridged to understand the interaction between migratory salmon and nutrient dynamics more fully. One key factor is the relationship between salmonid production and system trophic status. Plante and Downing (1993), using data from a large number of studies in lake systems, developed a quantitative relationship between P concentration in lakes and salmonine production. While several studies in rivers and streams indicate positive responses to nutrient addition (Johnston et al. 1990; Deegan and Peterson 1992; Griswold et al. 2003), a similar quantitative relationship between nutrient status and salmonid production in riverine systems has not been established. In addition, while we and others (Lyle and Elliott 1998) have investigated the amount of nutrients potentially transported by migratory Atlantic salmon, factors influencing the actual availability of these nutrients may ultimately determine their influence on stream ecosystems and fish production. Investigations on the pathways by which nutrients derived from Pacific salmon enter river and riparian food webs have revealed complex interactions between biological and physical factors occurring on a wide range of temporal and spatial scales (Willson and Halupka 1995; Cederholm et al. 2000). At present, these pathways in Atlantic salmon streams are essentially unknown. Future work should simultaneously apply our budget framework to other systems with appropriate and adequate data and focus on empirical investigations designed to refine parameter estimates and fill knowledge gaps.

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Regular papers

Articles ordinaires

Alternative model structures for bioenergetics budgets of a cruising predatory gadoid: incorporating estimates of food conversion and costs of locomotion

Niels G. Andersen and Jorgen Riis-Vestergaard

Abstract: Swimming costs of North Sea saithe (pollock) (*Pollachius virens*) were estimated from a balanced energy budget equation using field estimates of food ration and growth together with two alternative food conversion functions. Food ration estimates were obtained by application of a gastric evacuation model to field data on amount and composition of stomach contents. Laboratory-based net conversion efficiency, κ_{lab}, produced values of 1.61–6.72 of the activity multiplier, whereas estimates of 1.44–3.27 were obtained from application of an activity-modulated net conversion efficiency, κ_{mod}. The activity multiplier ranged from 2.0 to 2.5 at optimum cruising speed. The high activity levels obtained by application of κ_{lab} probably reflect low-cost accumulation of lipid in laboratory saithe. All together, the results indicated that net conversion efficiency in North Sea saithe was better described by κ_{mod} (ranging from 0.43 to 0.50) as opposed to κ_{lab} (0.51–0.76). Model estimates of food ration and body growth using activity costs at optimum cruising speed further demonstrated the sensitivity of estimates from the balanced energy budget equations to applied parameter values and field estimates of variables.

Résumé : Nous avons estimé les coûts de la nage chez la goberge (*Pollachius virens*) de la mer du Nord à l'aide d'une équation de bilan énergétique équilibré utilisant des estimations de terrain des rations alimentaires et de la croissance, ainsi que deux fonctions de rechange de conversion de la nourriture. Nous avons obtenu les estimations des rations alimentaires en appliquant un modèle d'évacuation gastrique à des données de terrain sur la quantité et la composition des contenus stomacaux. Un coefficient d'efficacité nette de conversion déterminé en laboratoire κ_{lab} donne des valeurs de 1,61–6,72 pour le multiplicateur du niveau d'activité, alors qu'un coefficient net d'efficacité modulé par le niveau d'activité κ_{mod} donne des valeurs de 1,44–3,27. Le multiplicateur du niveau d'activité varie de 2,0 à 2,5 à la vitesse de croisière optimale. Les forts niveaux d'activité obtenus par l'application de κ_{lab} indiquent probablement une accumulation à faible coût de graisse chez les goberges de laboratoire. Dans leur ensemble, les résultats indiquent que l'efficacité nette de conversion chez les goberges de la mer du Nord est mieux décrite par κ_{mod} (variant de 0,43 à 0,50) que par κ_{lab} (0,51–0,76). Les estimations du modèle de la ration alimentaire et de la croissance corporelle d'après les coûts de l'activité à la vitesse de croisière optimale montrent de plus la sensibilité des estimations provenant des équations de bilan énergétique équilibré aux valeurs appliquées aux paramètres et aux estimations des variables à partir de données de terrain.

[Traduit par la Rédaction]

Introduction

Reliable information about the amount and prey composition of food ingested by fishes is a prerequisite for successful studies of the trophic role of the fishes in the ecosystem. Estimation of food consumption rates of wild fish populations is usually based on gastric evacuation methods or by application of static energy budget (SEB) models. Gastric evacuation methods use stomach contents data together with information about gastric evacuation rate (Bajkov 1935; Elliott and Persson 1978; Pennington 1985). SEB models (Winberg 1956; Kitchell et al. 1977; Rice and Cochran 1984) may be expressed generally by the energy balance equation

$$(1) \qquad \kappa C = P_B + P_G + R_S + R_A$$

where P_B and P_G are the growth (energy increment) of body and gonads, respectively, net food conversion efficiency κ is the (net energy) fraction of food consumption C that is not lost as faeces, excretion, and apparent specific dynamic action (due to digestion, absorption, and processing of the ingested food), and R_S and R_A are the amounts of energy allocated to standard metabolism and swimming activity. Here, these energy budget models are categorized as being static because mechanisms for dynamic regulation of acqui-

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N.G. Andersen.[1] Department of Marine Ecology and Aquaculture, Danish Institute for Fisheries Research, North Sea Centre, P.O. Box 101, DK-9850 Hirtshals, Denmark.
J. Riis-Vestergaard. Department of Life Sciences, Aalborg University, North Sea Centre, DK-9850 Hirtshals, Denmark.

[1]Corresponding author (e-mail: nga@dfu.min.dk).

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sition and allocation of energy are not intrinsic features: the models are entirely data driven in this respect.

The energy balance equation may be solved for any of its terms when the others are known or estimated, although it is usually solved for growth or consumption. However, knowledge about the activity of wild fish is sparse, and activity costs are often considered using a simple multiple of standard or routine metabolism (e.g., Kitchell et al. 1977; Hansson et al. 1996; Schindler et al. 2002). In bioenergetics on salmonids, there is a tradition for using the activity multiplier $m_{A,opt} = (R_S + R_{A,opt})R_S^{-1}$, where $R_{A,opt}$ denotes the temperature and body size dependent activity costs at optimum cruising speed (e.g., Stewart et al. 1983; Beauchamp et al. 1989; Rand et al. 1993). Another approach to modelling activity costs, which has been used primarily on gadoids, is to couple them with food consumption rates (Ursin 1979; Majkowski and Waiwood 1981; Kerr 1982). It has, however, never been thoroughly justified that any choice of activity function is representative for the swimming costs in the wild. A third method for estimating activity costs has been to use empirical data on swimming velocity based on either telemetry in the wild or laboratory measurements (e.g., Rice and Cochran 1984; Stewart and Binkowski 1986; Essington et al. 2002). SEB models have also been used to estimate the amount of energy spent on activity by some freshwater species for which data on consumption were obtained by the gastric evacuation methodology (Boisclair and Leggett 1989; Trudel and Boisclair 1994). However, the activity estimates varied widely and unaccountably among populations (Boisclair and Leggett 1989).

Estimates of net conversion efficiency κ are usually based on results obtained from laboratory studies on somatic growth assuming that it applies to gonadal growth as well and that it is independent of the share of net energy allocated to swimming activity. However, the energy density and lipid content of well-fed gadoids in captivity are significantly higher than those of their wild conspecifics, even when the amounts of food available to the wild fish are not apparently limiting growth (Yaragina and Marshall 2000; Andersen and Riis-Vestergaard 2003). A large part of this difference may be ascribed to wild fish being more active as they feed, migrate, and spawn. The costs of de novo synthesis and deposition of proteins in the body from consumed proteins are large as compared with those of lipids (Reeds et al. 1982; Jobling 1985). Therefore, net conversion efficiency in wild gadoids may be substantially lower than predicted from laboratory experiments because part of the lipid that would otherwise be accumulated in the liver of laboratory fish is actually used to fuel the higher activity level of wild fish. In addition, the low lipid to protein ratio of pelagic eggs produced by the majority of marine fish species including gadoids (Riis-Vestergaard 2002) contributes to higher costs of energy accretion of wild fishes as compared with those estimated from experiments on somatic growth in the laboratory.

The aim of this study was to use an SEB model to estimate the costs of activity of North Sea saithe (pollock) (*Pollachius virens*) for which estimates of food consumption and growth were obtained independently of the model. The focus of the study was to evaluate the reliability of model estimates of activity costs applying a laboratory-based model of net conversion efficiency (Andersen and Riis-Vestergaard 2003) to wild fishes. As indicated above, net conversion efficiency in wild gadoids may be substantially lower than predicted from laboratory experiments, and estimated activity costs may thus be excessive. Therefore, an activity-modulated conversion model accounting for the difference in biochemical composition of biomass accretion between wild and laboratory fish was put forward as well and used to produce alternative estimates of activity costs. In addition, estimates of food ration and body growth were obtained from the SEB model fixing activity costs to those at optimum cruising speed. These were compared with field estimates to examine the sensitivity of output values from the SEB model to applied parameter values and field estimates.

Materials and methods

Parameterization of the SEB model

Maximum food consumption rate

Food consumption rate C (eq. 1) was expressed as maximum sustained consumption rate C_{max} (kilojoules per day) multiplied by actual feeding level f ranging from 0 to 1 (Kitchell et al. 1977). The C_{max} was parameterized for saithe as a function of temperature and body size (total length and mass) by Andersen and Riis-Vestergaard (2003). The laboratory fish used to establish these relationships were significantly fatter and attained a higher condition factor compared with those from the wild. Therefore, total length was applied as the effector variable in the present study, assuming that the maximum feeding capacity of the fish is coupled to structural body size rather than to amount of energy storage. The allometric length power of 1.61 obtained from the relatively few satiation experiments on saithe by Andersen and Riis-Vestergaard (2003) is low; C_{max} has been found to scale in proportion to body mass raised to the power 0.6–0.8 for the majority of fish species (Jobling 1994), which is equivalent to a length power of 1.8–2.4 assuming that body mass $M \propto$ total length L^3. The surface relationship L^2, advocated by, e.g., Ursin (1967) and found experimentally by Andersen and Riis-Vestergaard (2003) from an extensive data set on whiting (*Merlangius merlangus*), was adopted here. Accordingly, the parameters were reestimated by nonlinear regression (NLIN procedure) (SAS Institute Inc. 1990) from saithe data fixing the length power at the generalized value of 2. This resulted in the relationship $C_{max} = 0.0274L^2e^{0.087T}$ kJ·day^{-1}, where L is total length (centimetres) and T is temperature (degrees Celsius).

Net conversion efficiency

Net food conversion efficiency in North Sea saithe fed its major prey Norway pout (*Trisopterus esmarki*) at a range of ration levels in the laboratory was best described by a simple power function of food consumption rate (Andersen and Riis-Vestergaard 2003) as

$$\kappa_{lab} = 0.272C^{0.177} \quad (2)$$

Further, the mass-based lipid to protein ratio r_M of gross body energy production P_G^* (including the reserves used as sustenance by starved saithe) could be expressed as $1.87 - 3.14C^{-0.209}$ (Andersen and Riis-Vestergaard 2003). Multipli-

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cation with the ratio of lipid energy density 35.6 kJ·g^{-1} (Beamish et al. 1975) to protein energy density 24.0 kJ·g^{-1} (Jobling 1994) yields the energy-based lipid to protein ratio r_E of P_B^+

$$(3) \qquad r_E = 2.78 - 4.66C^{-0.209}$$

The laboratory-derived net conversion efficiency may then be expressed as a function of r_E combining eqs. 2 and 3

$$(4a) \qquad \kappa_{lab} = 0.997(2.78 - r_E)^{-0.845}$$

The lipid fraction of P_B^+ is $r_E(1 + r_E)^{-1}$ and gross lipid energy production $P_{B,lip}^+$ is $P_B^+ r_E(1 + r_E)^{-1}$. Gross protein energy production $P_{B,pro}^+$ is P_B^+(1 − lipid fraction) = $P_B^+[1 - r_E(1 + r_E)^{-1}] = P_B^+(1 + r_E)^{-1}$ assuming that lipids and proteins are the only biochemical components that contribute significantly to P_B^+.

Activity costs of wild saithe in surplus of activity costs of laboratory saithe are $R_{A*} = R_A - (R_{R(10)} - R_{S(10)})$, where $(R_{R(10)} - R_{S(10)})$ are the activity costs of laboratory fish estimated as the difference between routine metabolic rate $R_{R(10)} = 14.8M^{0.85}$ kJ·day^{-1} of saithe in the laboratory, obtained from growth experiments at 10 °C by Andersen and Riis-Vestergaard (2003), and mean standard metabolic rate $R_{S(10)} = 5.52M^{0.75}e^{0.8} = 12.3M^{0.75}$ kJ·day^{-1} of gadoids at 10 °C that is calculated in the below section. Thus, an activity-modulated net food conversion efficiency of wild saithe may be described as

$$(4b) \qquad \kappa_{wild} = 0.997[2.78 - (P_{B,lip}^+ - R_{A*})(P_{B,pro}^+ + R_{A*})^{-1}]^{-0.845}$$

where the consumption-dependent ratio $r_E = P_{B,lip}^+(P_{B,pro}^+)^{-1}$ (eq. 3) estimated from laboratory fish is corrected for the difference in biochemical composition of energy accretion between wild and laboratory fish assuming that any increased activity level is fuelled primarily by lipids.

Net conversion efficiencies described by eqs. 4*a* and 4*b* were used for running the SEB model in two scenarios to obtain alternative estimates of activity costs for saithe in the wild.

Standard metabolism

No data on standard metabolic rate of saithe are reported in the literature. Therefore, values from other gadoid species were used to express R_S as a function of body mass and temperature. The vast majority of the estimates of the mass power reported in the literature range from 0.6 to 0.9 (Brett and Groves 1979; Jobling 1994). The value 0.75 was recommended for interspecific comparisons by Feldman and McMahon (1983) and supported by physiological theory (West et al. 1997). Concerning the effect of temperature, Brett and Groves (1979) recommended a Q_{10} value of 2.3, which is equivalent to a temperature coefficient of 0.08 using an exponential relationship. Results on standard metabolic rate of Atlantic cod (*Gadus morhua*), whiting, and haddock (*Melanogrammus aeglefinus*) (Jones 1978; Bushnell et al. 1994; Schurmann and Steffensen 1997; J.-P. Herrmann, Institute of Hydrobiology and Fisheries Science, University of Hamburg, Olbersweg 24, D-22767 Hamburg, Germany, jpherrmann@rrz.uni-hamburg.de, personal communication) were recalculated to be $R_S = 5.52M^{0.75}e^{0.08T}$ kJ·day^{-1} as a mean figure using the above generalized parameter values of mass and temperature together with an oxycalorific coefficient of 13.6 kJ·g O_2^{-1} (Elliott and Davison 1975).

Costs of locomotion

Activity costs were expressed by the activity multiplier $m_A = (R_S + R_A)R_S^{-1}$, which eases intersize and interspecies comparisons. Based on reanalyses and a synthesis of results of other researchers, Beauchamp et al. (1989) parameterized optimum cruising speed of sockeye salmon (*Oncorhynchus nerka*) as $U_{opt} = 9.9M^{0.13}e^{0.0805T}$ cm·s^{-1} (M in grams) and corresponding total metabolic costs as $R_T = R_S + R_{A,opt} = R_S m_{A,opt} = 0.00143M^{0.791}e^{0.0867T}e^{0.0234U_{opt}}$ g O_2·day^{-1}. The standard metabolic rate R_S (at swimming speed $U = 0$) is thus $0.00143M^{0.791}e^{0.0867T}$ g O_2·day^{-1} or $4.59M^{0.791}e^{0.0867T}$ kJ·day^{-1} when M is expressed in kilograms and the oxycalorific coefficient is 13.6 kJ·g O_2^{-1}. This is similar to the above gadoid R_S for the ranges of body mass and temperature examined in the present study.

On a location in Loch Ewe, Sarno et al. (1994) used a fixed hydrophone array to obtain swimming speeds of patrolling schools of saithe that were tagged intragastrically with an acoustic transmitter. They found that the fishes swam with a mean speed of 22 cm·s^{-1} during light hours, which compares well with the optimum cruising speed of 28 cm·s^{-1} of this fish size (450 g) as calculated by the above relationship for sockeye salmon. Therefore, activity costs at optimum cruising speed of sockeye salmon were used as a standard of reference for our estimates of activity costs as well as an alternative, known variable to estimate consumption or growth from the energy budgets.

Field data

Food consumption rates

The principle of the gastric evacuation method is that the mean consumption rate of a population can be estimated from the instantaneous evacuation rate of the stomach contents of each individual in representative samples of the population over time by the expression

$$(5) \qquad \hat{C} = \overline{\rho S^{0.5}}$$

provided that the instantaneous gastric evacuation rate can be described by a square root function of the mass of stomach contents (Pennington 1985; Andersen 2001). The S and ρ are total mass and evacuation rate constant, respectively, of the stomach contents of each individual. The mean symbol denotes either a simple mean if sampling from the population is completely randomized or a more elaborated one in case of stratified sampling (typically by predator size, time of day, season, and geographical area).

The results from the stomach sampling project in 1991 undertaken by the International Council for Exploration of the Sea (ICES) (Hislop 1997)) were used to estimate food rations. The ICES saithe stomachs were pooled into predator length groups, and mean values of total mass and relative prey composition of stomach contents by age group for each quarter of the year were calculated for the total North Sea together with the mean length of saithe by age (Hislop 1997). However, estimation of consumption rates using eq. 5 requires that data from each individual stomach are avail-

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Table 1. Field data applied to the energy budget model of North Sea saithe.

	Body mass[a] ($M = aL^b$; kg)		Body energy density[b] ($E_D = a + bL$; $MJ \cdot kg^{-1}$)		Food consumption rate ($C = a + bA^c$; $MJ \cdot quarter^{-1}$)		
Quarter of the year	a ($\times 10^{-5}$)	b	a	b ($\times 10^{-2}$)	a	b ($\times 10^{-3}$)	c
1	2.30	2.78	3.49	2.64	0.750	45.9	2.67
2	1.33	2.90	3.70	1.24	2.663	18.4	3.53
3	1.17	2.94	4.06	2.55	2.577	5.43	4.23
4	0.95	3.01	3.55	3.13	2.265	49.7	3.16

Length at age	L (cm) = 13.02 + 8.23A (years)
Fecundity	$0.124L^{3.9}$ (no. of eggs per female)[c]
Egg energy	1.51 ($J \cdot egg^{-1}$)[b]
Age (years)	≤3, 4, 5, 6, ≥7
Maturity index	0, 0.15, 0.7, 0.9, 1

[a]J.R.G. Hislop (Fisheries Research Service, Marine Laboratory, Victoria Road, Aberdeen, AB11 9DB, Scotland, hislopjrg@marlab.ac.uk, personal communication).
[b]Pedersen and Hislop (2001).
[c]Storozhuk and Golovanov (1976).
[d]Hislop and Bell (1987).

able. Therefore, applying the methodology of Andersen (2001), quarterly consumption rate (grams per hour) by age was estimated as

$$\bar{C} = \bar{\rho} k \bar{S}^{0.5} = \bar{\rho}_E (\sum \bar{a}_i \bar{E}_i)^{-\mu} k \bar{S}^{0.5} = \bar{\rho}_E \bar{E}^{-\mu} k \bar{S}^{0.5} \quad g \cdot h^{-1} \tag{6}$$

where the quarterly mean gastric evacuation rate constant $\bar{\rho}$ was expanded as a function of body size, temperature, and prey energy density ($\bar{\rho}_E = \rho_{LTE} \bar{L}^{\lambda} e^{\delta \bar{T}}$). $\bar{L}$ is the mean length of saithe, $\bar{T}$ is the mean temperature, $\bar{E}$ is the mean energy density of the stomach contents, $\bar{E}_i$ is the mean energy density of prey type i, and $\bar{a}_i$ is the mean fraction made up by prey type i in the stomach contents. Values of the parameters δ, λ, μ, and ρ_{LTE} were estimated for saithe by Andersen (2001). The values of $S^{0.5}$ and $\bar{S}^{0.5}$ in eqs. 5 and 6, respectively, differ unless all values of S are equal (Ursin et al. 1985). Therefore, a factor k correcting for $S^{0.5} \neq \bar{S}^{0.5}$ forms part of eq. 6. An overall value of k calculated by Andersen (2001) from two sets of data on total contents of individual stomachs of saithe (using the expression $k = S^{0.5}/\bar{S}^{0.5}$) was applied in the present study.

The quarterly mean energy density $\bar{E}_i$ of prey type i was estimated from its size-class distribution in the saithe stomachs (extracted from the ICES 1991 stomach database (Hislop 1997)) and energy density by size-class (Pedersen and Hislop 2001).

Data on the geographical distribution (squares of 1° longitude and 0.5° latitude) of quarterly mean bottom temperature and abundance of saithe by age in 1991 were combined to estimate the mean temperature $\bar{T}$ experienced by North Sea saithe

$$\bar{T} = (\sum \bar{T}_j \bar{N}_{j,\mathrm{CPUE}}) / \sum \bar{N}_{j,\mathrm{CPUE}} \tag{7}$$

where $\bar{N}_{j,\mathrm{CPUE}}$ is the mean catch rate in numbers per unit effort (per hour of trawling) in the jth geographical square and $\bar{T}_j$ is the mean temperature at the mean catch depth in the jth square (Andersen 2001). Catch rates N_{CPUE} by age-class and trawling depth were acquired from the ICES International Bottom Trawl Survey database, Copenhagen. Values of $\bar{T}_j$ were calculated (by J.-P. Herrmann, Institute of Hydrobiology and Fisheries Science, University of Hamburg, Olbersweg 24, D-22767 Hamburg, Germany, jpherrmann@rrz.uni-hamburg.de, personal communication) from data obtained by application of a three-dimensional circulation model of the North Sea (Pohlmann 1996). Quarterly food rations (megajoules) were estimated as 2190 h × $\bar{C}$ $g \cdot h^{-1}$ × $\bar{E}$ $kJ \cdot g^{-1}$ × 10^{-3}.

Somatic growth and egg production

Total body energies at the start (and end) of each quarter for saithe of age 3–8 were calculated combining information about age–length, length–mass, and length – energy density relationships. Age–length data of North Sea saithe (Hislop 1997) were described by a linear function in the present study (Table 1; Fig. 1). Quarterly power functions relating saithe length to mass were based on unpublished Scottish data on commercial catches from the North Sea (Table 1) (J.R.G. Hislop, Fisheries Research Service, Marine Laboratory, Victoria Road, Aberdeen, AB11 9DB, Scotland, hislopjrg@marlab.ac.uk, personal communication). Pedersen and Hislop (2001) obtained quarterly relationships between energy density and total length from saithe sampled in the northern and central parts of the North Sea (Table 1). Maturing fishes with prominent gonads were never observed (J. Pedersen, EUC NORD, HTX, Haanbaekvej 50, DK-9900 Frederikshavn, Denmark, jep@eucnord.dk, personal communication). Therefore, the results were interpreted as representing energy density of the body only.

In the model, gonadal energy content was assumed to increase linearly from the first day of quarter 4 attaining the final value of annual energy accretion in gonads midquarter 1 the following year. The fecundity of a saithe by age (Table 1) was calculated from the age–length relationship of midquarter 1, where spawning peaks, and a power function relating fecundity to total length of saithe (Storozhuk and Golovanov 1976). Multiplication with maturity index (conventional values for saithe applied by ICES in the North Sea stock assessment) and mean energy content of a saithe egg

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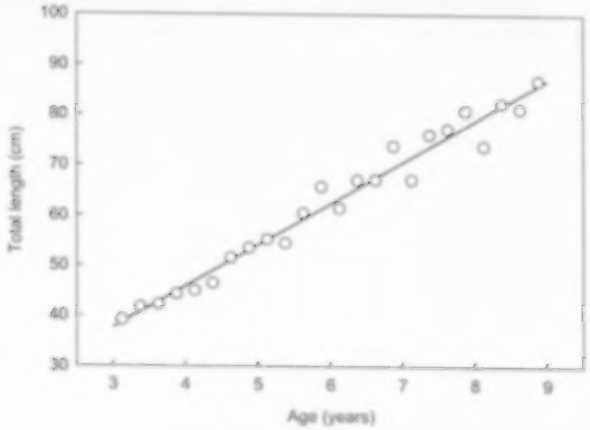
Fig. 1. Mean total length of North Sea saithe (pollock) (*Pollachius virens*) by age and quarter in 1991. The line is provided by linear regression.



(Hislop and Bell 1987) yielded a mean estimate of annual energy accretion in eggs of a saithe (Table 1). This value of total egg energy production was used here as a measure of total spawning investment for both sexes owing to the lack of appropriate information on males.

Estimation of energy budget terms

The parameterized SEB model was run in a spreadsheet macros programme on a quarterly basis by age group of North Sea saithe using the two alternative versions of net conversion efficiency described by eqs. 4*a* and 4*b*. Starting with known initial and final body lengths, the value of the constant feeding level f that resulted in the best fit between predicted and known quarterly food consumption was obtained iteratively by a loop projecting body length and associated maximum food ration C_{max} in 91 daily steps according to known growth trajectory. Subsequently, activity costs represented by the activity multiplier $m_A = (R_S + R_A)R_S^{-1}$ were estimated iteratively by another loop as the predicted, accumulated value of R_A that balanced eq. 1. The energy equation did not balance in all cases ($\kappa C < P_B + P_G + R_S$). Therefore, annual runs were performed as well to acquire separate, annual figures estimating f and m_A as constant values over the year. The effect of parameter uncertainty on estimated value of the activity multiplier m_A was evaluated by perturbation of an applied parameter value by ±10%. Sensitivity of the estimate was calculated as 100 $(m_{A^*} - m_A)m_A^{-1}$, where m_{A^*} was the estimate obtained from a perturbed parameter value.

Food consumption and body growth were estimated separately also from the energy equation as the only unknown variable using the activity costs fixed at optimum cruising speed together with the two alternative versions of net conversion efficiency.

Results

North Sea saithe feed on fishes and crustaceans. Norway pout and Atlantic herring (*Clupea harengus*) were the overall dominant fish prey in the stomachs. Atlantic herring gradually replaced Norway pout as the major prey with increasing size of saithe. The high energy densities of the stomach contents of older saithe in the third quarter of the year (Table 2) reflect the importance of fat autumn Atlantic herring in their diet. Sandeel (*Ammodytes marinus*), haddock, and whiting also formed a significant part of the stomach contents. Sandeel dominated this prey group in younger saithe, and whiting was the most important one in older saithe. Krill formed the dominant crustacean part of the stomach contents and amounted to almost half the total diet in saithe of age 3–4 in quarter 2. In general, the krill fraction constituted only 2%–10% of total stomach contents.

North Sea saithe of age 3+ were mainly distributed in the deeper parts of the northern North Sea. Accordingly, quarterly mean temperatures experienced by the saithe as estimated in the present study lay within a narrow range of 6–7 °C (Table 2). The quarterly food rations were generally low in quarter 1 of the year, whereas the pattern was more variable in the other seasons (Table 2). For each quarter, the relationship between food ration and age of saithe was smoothed by fitting a power function to the data (Table 1).

Annual gonadal production P_G of a saithe increased from 0.06 to 6.4 MJ with increasing age of saithe (Table 3). This way, the P_G to P_B ratio increased from 0.03 to 0.76. The overall increase of somatic energy P_B was exponential (Fig. 2). The intraannual growth trajectories showed a decrease in total energy during spawning (quarter 1) as well as a further drop subsequent to spawning (from quarter 1 to 2) followed by an increase until spawning next year (Fig. 2).

Reflecting the seasonal patterns of food rations, age-specific values of the feeding level f obtained from the first loop in quarterly runs of the model varied, being low in the first quarter of the year (Table 3). The overall annual f values increased from 0.41 for saithe of age 3 to 1.05 for the oldest saithe (Table 3). The f is independent of the version of net conversion that is used in the model runs because, being estimated from the first loop of the computer programme, it only depends on field-based food rations and projections of body length.

The annual estimates of net conversion efficiency κ_{lab} increased with increasing age of saithe from 0.51 to 0.76, while those of κ_{wild} were uniform, ranging from 0.43 to 0.50 (Table 3). The energy budget of the first quarter of the year obtained from κ_{lab} as well as κ_{wild} runs did not balance for younger saithe (Table 3). Meaningful estimates of net conversion efficiencies and activity costs of younger saithe could therefore not be obtained from these quarters. Where estimation was possible, the values of activity multiplier m_A obtained from quarter 1 were substantially lower than those of the other seasons (Table 3). The annual estimates of m_A ranged from 1.61 to 6.72 using κ_{lab} in the model runs, and κ_{wild} gave values that increased from 1.44 to 3.27 with increasing age of saithe (Table 3). The substantial difference between the values of m_A obtained for older saithe by use of the two net conversion versions was still maintained, perturbing the different model parameters (Table 4). The m_A estimates were changed by 18% at the most (by perturbation of food consumption rate).

The fraction of energy allocated to standard metabolism R_S decreased from 42% to 12% of net energy with increasing age of saithe applying κ_{lab} in the model runs, whereas activity expenditures R_A increased from 26% to 71%

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Table 2. Field estimates of total food ration of a North Sea saithe in 1991 (combining field data on stomach contents with a gastric evacuation model).

				Total stomach contents		
Age (years)	Quarter of the year	Total length $\bar{L}$ (cm)	Temperature $\bar{T}$ (°C)	Energy density $\bar{E}$ (kJ·g^{-1})	Mass $\bar{s}$ (g)	Food ration C (MJ)
3	1	39.2	6.8	5.0	3.19	1.629
	2	41.8	6.6	4.4	14.11	3.628
	3	42.3	6.9	4.6	9.31	3.090
	4	44.4	6.3	5.1	13.57	3.878
	1–4					12.225
4	1	45.1	6.8	5.1	5.04	2.515
	2	46.6	6.5	4.4	19.00	4.906
	3	51.6	6.7	5.1	15.15	5.252
	4	53.6	6.2	5.6	19.45	6.124
	1–4					18.797
5	1	55.3	6.8	6.0	12.50	5.426
	2	54.6	6.0	4.5	42.82	8.912
	3	60.6	6.9	5.8	16.80	7.209
	4	65.8	6.0	6.8	40.02	11.929
	1–4					33.476
6	1	61.6	6.6	6.1	15.35	6.941
	2	67.1	5.8	4.6	70.51	15.168
	3	67.2	7.1	6.7	17.05	8.725
	4	73.9	6.0	7.3	56.22	16.895
	1–4					47.729
7	1	67.2	6.6	6.2	19.22	8.818
	2	76.2	5.8	4.6	103.25	22.090
	3	77.3	7.1	10.1	161.80	34.848
	4	80.9	6.0	7.9	88.33	24.391
	1–4					90.147
8	1	73.9	6.6	6.2	22.65	10.976
	2	82.4	5.8	4.7	137.31	28.552
	3	81.3	7.1	10.2	230.40	44.788
	4	87.0	6.0	8.3	133.44	33.472
	1–4					117.788

(Fig. 3*a*). Body growth P_B decreased from 31% to 9%, and energy accumulated in gonads P_G increased from 1% to 7%. The age-related trends of energy allocation as estimated from the κ_{wild}-based runs were less pronounced (Fig. 3*b*). However, larger fractions of energy were put into body (16%) and gonads (12%) in the oldest saithe.

Independently of the applied version of net conversion, the model estimates of annual food ration using activity costs at optimum cruising speed $R_{A,opt}$ were higher for young saithe and lower for old saithe, respectively, as compared with the field values obtained by the gastric evacuation method (Fig. 4). Accordingly, the age-specific ranges of f estimates were lesser and almost independent of age using κ_{lab} in the model run. The age-specific trends in relative allocation of net energy were generally weak (Fig. 3*c*). The exception was the fraction allotted to gonads, which increased from 1% to 15% with increasing age of saithe (notice that the relative allocation of net energy does not depend on the choice of net conversion efficiency because food ration is the only unknown variable in this case applying activity costs fixed to be those at $R_{A,opt}$). The activity multiplier m_A increased from 2.0 to 2.5 as obtained from these model runs using activity costs $R_{A,opt}$ at optimum cruising speed to estimate food consumption.

Model estimates of body growth P_B using $R_{A,opt}$ and field estimates of food rations in the model runs were distinct from the values obtained from the field (Fig. 5). However, like the above model estimates of annual food ration, model values of P_B were similar to field estimates for medium-aged saithe.

Discussion

The age-specific, seasonal feeding level f varied, being low in the first quarter of the year and influencing the composition of the quarterly energy budgets. However, the annual feeding level increased steadily from 0.41 to 1.05 with increasing age of saithe. The entirely laboratory-based net conversion efficiency κ_{lab} increased correspondingly from 0.51 to 0.76, making a large fraction of net energy available

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Table 3. Quarterly and annual energy budgets for North Sea saithe.

Age (years)	Quarter of the year	f	C (MJ)*	P_B (MJ)	P_G (MJ)	R_S (MJ)	κ_{sub} κ	κ_{sub} R_A (MJ)	κ_{sub} m_A	κ_{wild} κ	κ_{wild} R_A (MJ)	κ_{wild} m_A
3	1	0.250	1.612	0.391	0	0.580	—†	—†	—†	—†	—†	—†
	2	0.506	3.554	0.379	0	0.593	0.519	0.874	2.47	0.426	0.542	1.91
	3	0.396	3.144	0.531	0	0.689	0.508	0.378	1.55	0.476	0.277	1.40
	4	0.465	3.870	0.598	0.062	0.753	0.527	0.628	1.83	0.474	0.422	1.56
	1–4	**0.410**	**12.181**	**1.899**	**0.062**	**2.616**	**0.506**	**1.590**	**1.61**	**0.470**	**1.148**	**1.44**
4	1	0.276	2.610	0.577	0.031	0.867	—†	—†	—†	—†	—†	—†
	2	0.509	5.125	0.550	0	0.877	0.554	1.412	2.61	0.441	0.833	1.95
	3	0.405	4.494	0.776	0	0.999	0.541	0.658	1.66	0.501	0.476	1.48
	4	0.541	6.251	0.881	0.544	1.091	0.574	1.072	1.98	0.512	0.681	1.62
	1–4	**0.438**	**18.481**	**2.786**	**0.575**	**3.834**	**0.546**	**2.889**	**1.75**	**0.498**	**2.009**	**1.52**
5	1	0.315	4.123	0.804	0.269	1.213	—†	—†	—†	0.595	0.168	1.14
	2	0.612	8.077	0.756	0	1.181	0.601	2.915	3.47	0.433	1.559	2.32
	3	0.493	7.506	1.078	0	1.410	0.593	1.962	2.39	0.483	1.138	1.81
	4	0.682	10.340	1.234	1.203	1.486	0.627	2.565	2.73	0.512	1.368	1.92
	1–4	**0.530**	**30.049**	**3.873**	**1.472**	**5.291**	**0.595**	**7.236**	**2.37**	**0.495**	**4.241**	**1.80**
6	1	0.367	6.238	1.073	0.595	1.595	0.574	0.316	1.20	0.604	0.508	1.32
	2	0.764	12.972	0.998	0	1.556	0.653	5.919	4.80	0.420	2.893	2.86
	3	0.660	13.241	1.438	0	1.908	0.656	5.334	3.80	0.445	2.549	2.34
	4	0.854	16.641	1.663	2.151	1.973	0.683	5.572	3.82	0.450	2.526	2.28
	1–4	**0.668**	**49.092**	**5.173**	**2.746**	**7.032**	**0.649**	**16.892**	**3.40**	**0.475**	**8.378**	**2.19**
7	1	0.417	9.033	1.389	1.064	2.056	0.613	1.026	1.50	0.608	0.981	1.48
	2	0.949	20.432	1.277	0	2.012	0.708	11.174	6.55	0.420	5.290	3.63
	3	0.914	23.052	1.862	0	2.459	0.723	12.349	6.02	0.420	5.359	3.18
	4	1.053	25.673	2.174	3.287	2.538	0.737	10.923	5.30	0.481	4.341	2.71
	1–4	**0.842**	**78.194**	**6.703**	**4.351**	**9.066**	**0.704**	**34.934**	**4.85**	**0.451**	**15.162**	**2.67**
8	1	0.467	12.580	1.753	1.625	2.578	0.650	2.216	1.86	0.603	1.633	1.63
	2	1.171	31.141	1.596	0	2.533	0.763	19.623	8.75	0.420	8.948	4.53
	3	1.245	38.606	2.353	0	3.086	0.792	25.147	9.15	0.420	10.773	4.49
	4	1.274	37.978	2.774	4.818	3.184	0.790	19.225	7.04	0.465	6.882	3.16
	1–4	**1.052**	**120.305**	**8.478**	**6.443**	**11.381**	**0.760**	**65.085**	**6.72**	**0.433**	**25.825**	**3.27**

Note: Figures in bold are obtained from annual model runs.
*Smoothed values obtained from the equations in Table 1.
†Unbalanced energy budget (net energy $\kappa C < P_B + P_G + R_S$).

for swimming activity of older saithe, which caused the activity multiplier m_A to increase from 1.61 to 6.72. In contrast, the activity multiplier obtained by use of the activity-modulated conversion efficiency κ_{wild} ranged from 1.44 to 3.27 only, and the conversion efficiency itself was at a relatively constant level of 0.43–0.49. The activity multiplier at expenditures of optimum cruising speed $R_{A,opt}$ increased from 2.0 to 2.5. The model estimates of activity as well as the model estimates of food consumption and body growth using the activity level of $R_{A,opt}$ demonstrated the sensitivity of SEB model estimates to applied parameter values and field estimates of variables.

The energy budget of the first quarter of the year did not balance for younger saithe, and the activity expenditures estimated from older saithe were substantially lower than those obtained from the other seasons. These features were probably caused by using an average length increment throughout the year while applying a linear growth curve. In contrast, field estimates of consumption rates were calculated on a quarterly basis that incorporated seasonal variability. The food rations of the first quarter of the year were consistently low as compared with those of the other quarters, indicating that the real length increment was lower than predicted by the annual average. Reduced food intake and growth is a common feature among temperate fishes during overwintering and spawning. In some species, feeding and growth stop during the spawning period, and this may even apply to immature individuals (van der Veer et al. 2001). The field estimates of somatic growth that enter the first-quarter model runs are, therefore, probably too high, leaving less room for activity costs to balance the energy equation for older saithe and even resulting in negative values of the estimates of activity costs for the younger ones (unbalanced equation). The seemingly unrealistic length increment estimates used in the first-quarter runs also influence the results from the following quarters of the year, biasing the modelling of seasonal dynamics of energy allocation in general. The present length increment data were,

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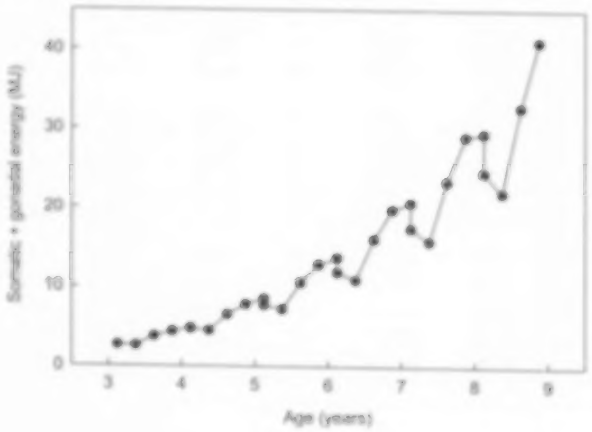
Table 4. Effect of perturbation of static energy budget (SEB) model parameters by ±10% on estimated value of activity multiplier m_A.

Model parameter	Effect on m_A (±%) by age (years) of saithe					
	3	4	5	6	7	8
Modelling performed by application of κ_{lab}						
Food consumption rate C	18	18	17	16	15	14
Net conversion κ	15	15	14	13	13	12
Body increment P_B	5	4	3	2	2	1
Gonadal increment P_G	<1	1	1	1	1	1
Standard metabolic rate R_S	10	10	10	10	10	10
Modelling performed by application of κ_{wild}						
Food consumption rate C	11	10	9	9	10	11
Net conversion κ	10	9	8	9	8	6
Body increment P_B	3	3	2	2	1	2
Gonadal increment P_G	<1	1	1	1	1	1
Standard metabolic rate R_S	7	7	8	8	9	9

Fig. 2. Total energy of a North Sea saithe (pollock) (*Pollachius virens*) by age and quarter. The lower value in quarter 1 represents postspawning somatic energy and the upper value includes the energy of eggs.



however, not sufficient to enable a higher temporal resolution. Therefore, results from the annual runs of the SEB model only were considered below.

The values between 5 and 7 of the activity multiplier m_A that were obtained from older saithe using the entirely laboratory-based net conversion efficiency κ_{lab} are rather extreme as compared with generally accepted values of 2–3 for mean activity levels of comparable cruising fish species like salmonids (Stewart et al. 1983; Beauchamp et al. 1989; Rand et al. 1993). Application of activity costs at optimum swimming speed in the present study resulted in m_A values that increased from 2 to 2.5 with increasing body size of saithe. The activity multiplier estimates obtained from the model runs applying activity-modulated net conversion efficiency κ_{wild} lie between 1.5 and 3, which (unlike the results obtained by the use of κ_{lab}) compares well with the above range reported in the literature as well as with the costs at optimum swimming speed. The results from application of κ_{wild} are further in accordance with the activity of the saithe that cruised around in Loch Ewe at daytime at optimum cruising speed and showed a little lower activity level during night (Sarno et al. 1994). Using κ_{lab}, the older saithe should spend 15%–25% of their time at maximum sustained swimming speed to balance the energy equation in the present study provided that the saithe swam at optimum cruising speed during the remaining part of the time. The literature information indicates that such an activity level is unrealistic (Videler 1993). North Sea saithe were tracked diurnally from a drifting vessel using a split-beam echosounder (Pedersen 2001). The mean body size was similar to that of the Loch Ewe study. However, the vast majority of swimming speeds ranged from 50 to 200 cm·s^{-1} with a mean of 105 cm·s^{-1}, which is close to the maximum sustained swimming speed found for this species by He and Wardle (1988). The upper range is close to the maximum burst speed of saithe reported by Videler (1993). The method of Pedersen (2001) did not allow for measurements on schooling saithe because single targets could not, then, be discriminated, and he suggested that the observed high swimming speeds were related to foraging behaviour, which lasts for very short periods of time only. Thus, the high activity multiplier values obtained from older saithe by application of κ_{lab} probably reflect the low-cost accumulation of lipid in larger laboratory saithe at high food rations (Andersen and Riis-Vestergaard 2003) giving an excessive surplus of net energy for activity as output from the model runs. This indicates that net conversion efficiency of North Sea saithe is described better by the activity-modulated functional relationship presented here as opposed to the values obtained directly from the laboratory by Andersen and Riis-Vestergaard (2003) and that conversion efficiency values of 0.65–0.75 are excessive for wild saithe, whereas values of 0.45–0.50 seem more realistic. Brett and Groves (1979) calculated the net conversion efficiency of a general carnivorous fish fed well above maintenance to be 0.59, while values of 0.62 and 0.67, respectively, can be obtained from the parameter values applied in bioenergetics studies on Atlantic cod by Hansson et al. (1996) and Krohn et al. (1997). Unlike saithe, Atlantic cod are not cruisers and are thus less active. Therefore, net

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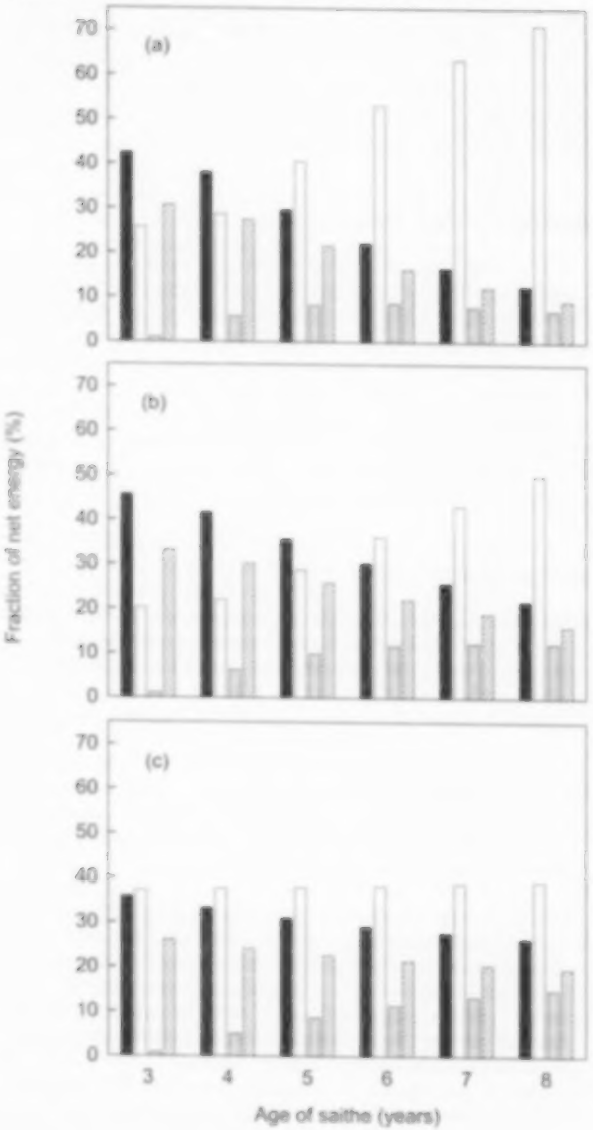
Fig. 3. Predicted allocation of net energy in North Sea saithe (pollock) (*Pollachius virens*) into standard metabolism (solid bars), activity expenditures (open bars), gonads (shaded bars), and soma (hatched bars) according to a static energy budget (SEB) model using (*a*) entirely laboratory-based and (*b*) activity-modulated versions of net conversion efficiency to estimate activity expenditures. (*c*) Allocation of net energy estimating food rations while activity expenditures are fixed to be those at optimum cruising speed (relative allocation is independent of the applied version of net conversion efficiency in this case).



conversion efficiencies of wild Atlantic cod may be higher than those of saithe, although the low energy density (liver index) of wild Atlantic cod as compared with their conspecifics kept in captivity tells against that.

Fig. 4. Field (solid) and model estimates of annual food ration (circles) and feeding level (bars) of North Sea saithe (pollock) (*Pollachius virens*) fixing the activity expenditures of the static energy budget model runs to be those at optimum cruising speed and using entirely laboratory-based (open) and activity-modulated (shaded) versions of net conversion efficiency.

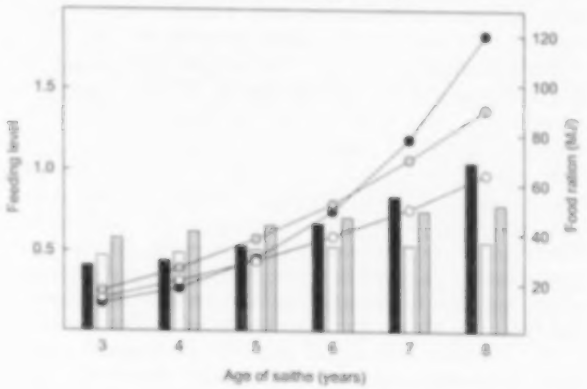
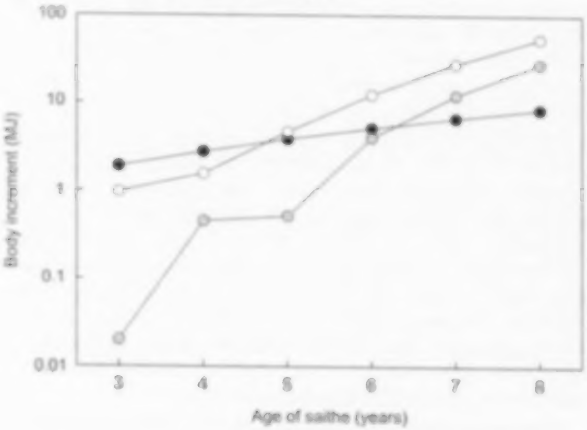


Fig. 5. Field (solid circles) and model estimates of annual body increment of North Sea saithe (pollock) (*Pollachius virens*) fixing the activity expenditures of the static energy budget model runs to be those at optimum cruising speed and using entirely laboratory-based (open circles) and activity-modulated (shaded circles) versions of net conversion efficiency.



Optimum cruising speed U_{opt} depended slightly on body size by $U_{opt} \propto M^{0.13}$ as opposed to the field estimates of food consumption rate C_{field} that increased heavily with increasing age (or size). This explains the significant trends over age of the allocation of energy obtained by application of C_{field} to the model runs as compared with the weak relationships originating from the application of U_{opt} to predict C from the model. The use of κ_{lab} rather than κ_{wild} further increases the allometric relationship because high κ_{lab} values are associated with high consumption rates and thus superimpose the allometry of consumption rate itself. The above allometric characteristics were reflected also in the results from comparing field and model estimates of somatic growth and food consumption. Model estimate of somatic

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growth constitutes a minor fraction of consumption rate and is calculated as the residual energy when all other terms are accounted for. The percent differences between model and field estimates of somatic growth were therefore up to one order of magnitude higher than those of consumption rate. The relative differences between model and field estimates of growth and consumption rates obtained here compare well with the results from studies compiled by Ney (1993).

The allocation of ingested food to body protein and lipid and, consequently, the net conversion efficiency depend on ration level as well as protein to lipid ratio of the diet, as for example shown for salmonids (Lee and Putnam 1973; Walton and Cowey 1982). Mostly, general values of defecation, excretion, and specific dynamic action are used as constituents of net conversion efficiency to the SEB models, which means that food composition is really not taken into consideration, although in some studies, different parameter values are used to discriminate between defecation loss of fish and invertebrate prey, as introduced by Stewart et al. (1983). Whereas SEB models generally are regarded as relatively insensitive to changes in parameter values of defecation and excretion, the results of Bajer et al. (2003) strongly suggest that substantially inaccurate defecation and excretion parameter values may result in significant errors in growth and consumption predictions. In the present study, prey composition and thus prey energy density varied between quarters and age groups of saithe. The extreme case was the dominant fraction of fat Atlantic herring in the diet of older saithe during the third quarter of the year as reflected by the high mean energy density of the stomach contents. The validity of the field-based estimates of food consumption rates is difficult to evaluate. They were based on a relatively large set of pooled data on mass and prey composition of stomach contents as well as on a gastric evacuation model. As demonstrated by Andersen (2001), application of pooled stomach data to the evacuation model applying the methodology of the present study does not appreciably influence the estimate of total energy ration, whereas the calculated prey composition may be considerably biased if the prey are of significantly different energy densities. However, both versions of net conversion efficiency applied in the present study were based on saithe fed their main prey, Norway pout, which in general was representative of the diet of North Sea saithe.

The present study demonstrates possible consequences of uncritical application of laboratory-derived values of physiological variables to situations in the wild as well as the sensitivity of SEB model estimates to applied parameter values and field estimates of variables. Successful efforts have been made to validate SEB model outputs for some well-investigated fresh water species by use of other variables. Madenjian et al. (2000) used, for example, the field and laboratory estimates of assimilation efficiency of polychlorinated biphenyls in lake trout (*Salvelinus namaycush*) to validate food consumption estimates by the Wisconsin bioenergetics model (Stewart et al. 1983). Being almost entirely data driven, SEB models are, however, by nature very data demanding. For many commercially important marine fish stocks, scarcity of field information as well as estimates of parameters describing relevant physiological variables reduces therefore, at present, the usability of SEB models to predict long-term consumption or growth, as was pointed out also by Ney (1993). Acquisition of adequate data to feed the SEB models is probably not always cost-effective for marine fish stocks. An alternative approach may be to reduce the demand for external as well as internal information about the fishes. This could be done by use of models with variables describing the nutritional and reproductive states of the animal together with inherent rules for food acquisition, allocation of ingested energy, onset of maturation, etc.; state-dependent rules for how ingested energy is allocated to reserves (lipid) and structural growth (protein) would, for example, be relevant in the present study. A simple, general framework of such dynamic energy budget models has been established by Kooijman (1993, 2000) and was applied to marine flatfishes by van der Veer et al. (2001).

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Migration and rearing histories of chinook salmon (*Oncorhynchus tshawytscha*) determined by ion microprobe Sr isotope and Sr/Ca transects of otoliths

Charles R. Bacon, Peter K. Weber, Kimberly A. Larsen, Reginald Reisenbichler, John A. Fitzpatrick, and Joseph L. Wooden

Abstract: Strontium isotope and Sr/Ca ratios measured in situ by ion microprobe along radial transects of otoliths of juvenile chinook salmon (*Oncorhynchus tshawytscha*) vary between watersheds with contrasting geology. Otoliths from ocean-type chinook from Skagit River estuary, Washington, had prehatch regions with $^{87}Sr/^{86}Sr$ ratios of ~0.709, suggesting a maternally inherited marine signature, extensive fresh water growth zones with $^{87}Sr/^{86}Sr$ ratios similar to those of the Skagit River at ~0.705, and marine-like $^{87}Sr/^{86}Sr$ ratios near their edges. Otoliths from stream-type chinook from central Idaho had prehatch $^{87}Sr/^{86}Sr$ ratios ≥0.711, indicating that a maternal marine Sr isotopic signature is not preserved after the ~1000- to 1400-km migration from the Pacific Ocean. $^{87}Sr/^{86}Sr$ ratios in the outer portions of otoliths from these Idaho juveniles were similar to those of their respective streams (~0.708–0.722). For Skagit juveniles, fresh water growth was marked by small decreases in otolith Sr/Ca, with increases in Sr/Ca corresponding to increases in $^{87}Sr/^{86}Sr$ with migration into salt water. Otoliths of Idaho fish had Sr/Ca radial variation patterns that record seasonal fluctuation in ambient water Sr/Ca ratios. The ion microprobe's ability to measure both $^{87}Sr/^{86}Sr$ and Sr/Ca ratios of otoliths at high spatial resolution in situ provides a new tool for studies of fish rearing and migration.

Résumé : Les concentrations de l'isotope de strontium et les rapports Sr/Ca mesurés à l'aide d'une microsonde ionique le long de coupes radiales d'otolithes de jeunes saumons quinnat (*Oncorhynchus tshawytscha*) varient en fonction des caractéristiques géologiques des bassins versants. Les otolithes de saumons de type océanique de l'estuaire de la Skagit, Washington, possèdent des régions antérieures à l'éclosion avec des rapports $^{87}Sr/^{86}Sr$ de ~0,709 indiquant une signature marine héritée de la mère, des zones importantes de croissance en eau douce avec des rapports $^{87}Sr/^{86}Sr$ de ~0,705 semblables à ceux de la Skagit et des rapports de type marin près des marges. Les otolithes de saumons de type rivière du centre de l'Idaho ont des rapports $^{87}Sr/^{86}Sr$ avant l'éclosion de ≥0,711, ce qui indique que la signature Sr maternelle marine ne s'est pas conservée après une migration de ~1000–1400 km depuis le Pacifique. Les rapports $^{87}Sr/^{86}Sr$ des zones externes des otolithes de ces jeunes saumons de l'Idaho correspondent à ceux de leurs cours d'eau respectifs (~0,708–0,722). Chez les jeunes saumons de Skagit, la croissance en eau douce s'accompagne de faibles diminutions de Sr/Ca dans les otolithes; la migration en eau salée amène un accroissement de Sr/Ca correspondant à l'augmentation de $^{87}Sr/^{86}Sr$. Les otolithes des poissons d'Idaho affichent des patrons de variation radiale de Sr/Ca qui reflètent les fluctuations saisonnières des rapports Sr/Ca dans l'eau du milieu. La capacité des microsondes ioniques à mesurer les rapports $^{87}Sr/^{86}Sr$ et Sr/Ca des otolithes à une forte résolution spatiale in situ fournit un nouvel outil pour étudier l'élevage et la migration des poissons.

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C.R. Bacon.[1] US Geological Survey, MS 910, 345 Middlefield Road, Menlo Park, CA 94025, USA.
P.K. Weber.[2] Department of Geography, University of California, Berkeley, CA 94720, USA.
K.A. Larsen and R. Reisenbichler. US Geological Survey, Western Fisheries Research Center, 6505 NE 65th Street, Seattle, WA 98115, USA.
J.A. Fitzpatrick. US Geological Survey, MS 420, 345 Middlefield Road, Menlo Park, CA 94025, USA.
J.L. Wooden. US Geological Survey, Stanford–USGS Ion Microprobe Laboratory, Green Earth Science Research Building, Stanford, CA 94305, USA.

[1]Corresonding author (email: cbacon@usgs.gov).
[2]Present address: Chemical Biology and Nuclear Science, Lawrence Livermore National Laboratory, L-231, P.O. Box 808, Livermore, CA 94551-0808, USA.

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Introduction

The minor and trace element chemistry of calcified tissues has been used extensively for reconstruction of animal migration. Isotopic tracers may be more sensitive than elemental markers in cases where there are confounding effects of biological mediation of elemental uptake or seasonal variation in environmental chemistry. Otoliths display incremental growth patterns that preserve records of environmental water chemistry and food sources that are not affected by chemical changes after precipitation (Kalish 1990; Campana 1999). The otoliths of fish are composed of ~95% aragonite plus ~5% protein-rich organic matrix. Otoliths grow in the inner ear by addition of concentric layers that form rings or growth increments in cross section (Fig. 1). Each increment consists of an aragonite-rich incremental zone and a thinner, protein-rich discontinuous zone (Campana and Neilson 1985). The center or nucleus of an otolith is formed of one or more primordia that are the loci of calcification. Prominent, optically opaque rings or checks commonly form when the egg hatches (hatch check) and as the yolk sac is fully consumed (emergence check) at the first feeding (Marshall and Parker 1982; Campana and Neilson 1985). Following emergence, growth generally produces more uniform, concentric increments. Typical growth increments likely reflect diel cycles but subdiel increments, commonly related to feeding, are known from experimental work (e.g., Marshall and Parker 1982; Neilson and Geen 1982).

Anadromous fish spend much of their lives in the sea and migrate to fresh water to spawn. The use of otolith microchemistry to reconstruct the chronology of migrations between fresh water, estuary, and seawater is becoming a standard tool in the study of fishes (Campana 1999). Many studies of minor or trace element concentrations using various microbeam techniques (e.g., electron microprobe, laser-ablation inductively coupled plasma mass spectrometry (LA-ICP-MS), proton-induced X-ray excitation) have shown that otolith composition tracks the environment in which the fish was living at a particular time in its life (e.g., Campana et al. 1997; Secor and Rooker 2000; Wells et al. 2003). Among elements known to substitute for Ca in aragonite, Sr occurs in salmonid otoliths in hundreds of parts per million (ppm) and is present approximately in proportion to its concentration relative to Ca in the environment (Kalish 1990; Rieman et al. 1994; Zimmerman and Reeves 2002). Strontium concentration in otoliths typically is expressed as the Sr/Ca ratio in mmoles per mole. Time spent in fresh water and seawater (Sr/Ca ~8.8 mmol·mol^{-1}) by anadromous fishes often can be determined by measuring Sr concentration or Sr/Ca ratios along radial transects of sectioned otoliths (e.g., Rieman et al. 1994; Zimmerman and Reeves 2000; Volk et al. 2000). However, in watersheds characterized by high ambient Sr/Ca, the method is incapable of discriminating between marine and fresh water otolith growth (Rieman et al. 1994). Ambiguities in interpretation also may arise from physiological effects on Sr/Ca ratios of otoliths (Sadovy and Severin 1994; Campana 1999).

The isotopic compositions of otoliths in many cases have the potential to reveal environmental differences in modern fish habitat or provenance of fossil otoliths with greater certainty than do trace element concentrations. In the case of Sr, biological processes and concentrations of Sr and Ca in environmental water will not affect isotopic composition measured in the otolith (conceivably, biological fractionation of Sr isotopes might be detected by methods substantially more precise than that employed here). For example, Kennedy et al. (1997) and Ingram and Weber (1999) showed that the Sr isotopic compositions of whole otoliths from juvenile salmon reflect $^{87}Sr/^{86}Sr$ ratios of natal streams. Thorrold and Shuttleworth (2000) reported $^{87}Sr/^{86}Sr$ ratios measured in situ in steelhead (*Oncorhynchus mykiss*) and weakfish (*Cynoscion regalis*) otoliths by laser-ablation sector-field ICP-MS with the laser beam rastered over an area 100 µm × 200 µm. Klaue et al. (2000) used micromilling and thermal ionization mass spectrometry (TIMS) to determine $^{87}Sr/^{86}Sr$ ratios in sets of otolith growth increments of Atlantic salmon (*Salmo salar*). Recently, Weber et al. (2002) demonstrated that the isotopic composition of S ($^{34}S/^{32}S$), sequestered in the organic matrix of salmon otoliths and measured in situ by secondary ion mass spectrometry (SIMS), or ion microprobe, can discriminate between otolith growth increments of fish ingesting either river or marine/hatchery diets. Here, we use a similar approach and determine Sr isotopic composition of salmon otoliths in situ by SIMS, which has the advantage over other methods in having high spatial resolution (maximum ~25 µm × 35 µm for Sr isotopic analysis) and low depth penetration (~2 µm).

Strontium occurs as isotopes of masses 84, 86, 87, and 88. The reported isotopic composition of Sr varies in rocks because ^{87}Sr is the daughter product of β-decay of ^{87}Rb (half-life 48.8×10^9 years; Steiger and Jäger 1977). The $^{87}Sr/^{86}Sr$ ratio of a rock thus depends on the Rb/Sr ratio and time so that ancient rocks have present-day $^{87}Sr/^{86}Sr$ ratios higher than younger or lower Rb/Sr rocks of similar initial $^{87}Sr/^{86}Sr$. Dissolved Sr in surface water (i.e., streams and rivers) has an isotopic composition that integrates all upstream sources. Although contributions from different portions of a watershed will vary depending on minerals

Fig. 1. Transmitted light photomicrograph of polished thin section of sagittal otolith 1.7 mm long from a juvenile chinook salmon (specimen 86-28-08) collected from the South Fork of the Salmon River, Idaho. Ion probe craters (~30 µm in diameter) are surrounded by bright rings (~45 µm in diameter) where gold conductive coating was removed by rastering the primary ion beam prior to analysis. HC indicates hatch check.

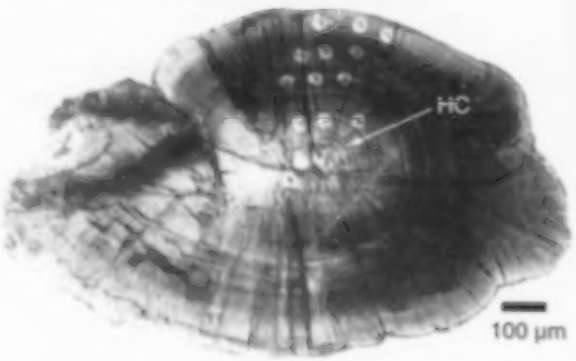

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Table 1. Locations, collection dates, Sr and Ca concentrations, Sr/Ca mole ratios, and $^{87}Sr/^{86}Sr$ ratios of filtered water samples.

Location	Latitude (°N)	Longitude (°W)	Collection date	Sr (μg·L^{-1})	Ca (mg·L^{-1})	Sr/Ca (mmol·mol^{-1})	$^{87}Sr/^{86}Sr$ (±0.00002)
Skagit River, Washington	48°26.8′	122°20.5′	2 May 2002	36	6.9	2.4	0.70533
South Fork Salmon River, Idaho	44°37.4′	115°41.3′	4 June 2002	37	2.7	6.3	0.70802
			24 Sept. 2003	87	4.9	8.1	0.70807
Herd Creek, Idaho	44°08.3′	114°16.9′	6 June 2002	248	19.7	5.8	0.70955
			23 Sept. 2003	348	22.2	7.2	0.70952
American River, Idaho	45°50.6′	115°24.8′	19 July 2002	33	2.6	5.8	0.72157
			25 Sept. 2003	38	2.7	6.4	0.72170
Sea water[a]	—	—	—	7900	412	8.8	0.7092

[a]Concentrations from Libes (1992), Table 3.5.

consumed in weathering and soil formation, the $^{87}Sr/^{86}Sr$ ratio of dissolved Sr in a fresh water sample is characteristic of the geology of the entire watershed that contributes to the sampling site. For example, the $^{87}Sr/^{86}Sr$ ratios of fresh waters analyzed in the present study by TIMS (Table 1) range from 0.70533 ± 2 (±0.0002 external precision) in the Skagit River that flows through the continental margin in Washington to 0.72170 ± 2 in the American River that drains Precambrian metasedimentary rocks in central Idaho. Studies of $^{87}Sr/^{86}Sr$ time series in river waters from France (Semhi et al. 2000; Grosbois et al. 2000) have shown ranges of up to ~0.001 that commonly are correlated with differences in discharge, although anthropogenic inputs to the Sr budget in these rivers may be more significant than in our examples. In contrast, Sr is well mixed in the modern oceans and is effectively invariant at an $^{87}Sr/^{86}Sr$ ratio of 0.7092. The high Sr concentration in seawater in comparison with river waters (Table 1) means that Sr in mixed waters of estuaries will be dominated by the marine $^{87}Sr/^{86}Sr$ ratio. This also is true of Sr/Ca ratios.

To be a valid environmental indicator, the measured $^{87}Sr/^{86}Sr$ ratio of the outermost growth increment(s) of an otolith should be within error of the value for ambient water at the collection site. This established, variation in $^{87}Sr/^{86}Sr$ ratios among interior growth increments can be used to characterize habitats during the life of the fish and, in the prehatch region, as a maternal fingerprint. The precision required for the method to be useful, assuming that $^{87}Sr/^{86}Sr$ ratios are accurate, of course depends on the range in $^{87}Sr/^{86}Sr$ ratios of the environments in question but must have external precision on the order of ±0.001 (1σ, standard error) or better in $^{87}Sr/^{86}Sr$ for many applications.

We used the sensitive high-resolution ion microprobe with reverse geometry (SHRIMP RG) jointly operated by the US Geological Survey (USGS) and Stanford University (http://shrimprg.stanford.edu) to determine Sr isotopic compositions and Sr/Ca elemental ratios in situ in otoliths from juvenile chinook salmon (*Oncorhynchus tshawytscha*) with a spatial resolution of ~30 μm. The goal of our study was to use $^{87}Sr/^{86}Sr$ ratios to monitor fish habitat during the first year of life by comparison with seawater and analyzed surface waters from watersheds with contrasting geology.

Methods

Specimens were selected from existing collections at the USGS Western Fisheries Research Center (Seattle, Washington) to represent wild juveniles from river systems within regions of different geologic history and lithologic character (Fig. 2). Four otolith samples were from juveniles collected within the Skagit Bay and estuary where the Skagit River drains into the Pacific Ocean via Puget Sound (Fig. 3*a*). Three other samples were collected near their natal areas in the state of Idaho (Fig. 3*b*) as much as 1400 km up the Columbia–Snake River system from the marine environment (Fig. 2). Skagit fish are ocean-type chinook that migrate from natal streams to the sea within a few months of hatching, whereas the Idaho fish are stream-type chinook that spend a full year in fresh water (Healey 1991). The Skagit River traverses comparatively youthful and low-$^{87}Sr/^{86}Sr$ igneous and metamorphic rocks of the Cascades Range. The Idaho streams are located on the North American craton in rocks with variable, but comparatively high, $^{87}Sr/^{86}Sr$ ratios (e.g., Fleck and Criss 1985).

Otoliths were removed from specimens of wild juvenile chinook salmon preserved in 95% ethanol (Table 2), stored in 95% ethanol, embedded in thermal resin, mounted on glass slides, sectioned along the longitudinal (sagittal) plane, polished, and coated with ~10 nm of gold. This protocol is unlikely to result in measurable effects on Sr concentration or isotopic composition (Milton and Chenery 1998; Proctor and Thresher 1998). Sagittal otoliths, the largest of the three pairs of otoliths in teleost fishes, were used in this study. The sagittal otoliths of juvenile fish measured ~1.3–3.0 mm in length (Table 2). Transects from primordia to the edge of the otolith were located in sectors of otoliths where growth increments were well defined (Fig. 1). Transect lengths were ~0.5–1.1 mm (Table 2).

Ion microprobe analyses were performed on ~15 spots in each transect, generally starting in the central region as closely as possible to centers of primordia and moving to the edge in groups of 2–4 spots (typically three) per growth region. Because of increment width variation within individual otoliths in our study (~1.5–6 μm), each ion microprobe analysis sampled growth increment sets representing between one and three weeks, assuming each increment represents 24 h. We were able to confine the ion probe beam entirely to a primordium only in three instances because of the small size of primordia and the presence of pits in their centers. In all cases, however, the innermost transect points sampled material well inside of the hatch check and is therefore expected to have been inherited maternally. Analytical results are plotted in the figures against normalized radial distance (r) from the center to the edge of the otolith. Transect lengths are approximate because replicate analysis sites are distributed

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Fig. 2. Selected river systems in the US Pacific Northwest. (*a*) Skagit River drainage. (*b*) Central Idaho. Wide river traces are Skagit River drainage in area of figure and Columbia–Snake–Salmon/Clearwater migration routes to Idaho sites. Fish collection and water sampling sites (circles): A, American River; C, Clearwater River near Spalding; S, South Fork Salmon River; H, Herd Creek; V, Skagit River near Mount Vernon; W, Salmon River at White Bird. C, V, and W are USGS National Stream Quality Accounting Network (NASQAN) sites; V also is very close to our Skagit River water sample locality.

along different azimuths within growth regions (e.g., Fig. 1).

The ion microprobe employs a focused primary beam of ions that sputters atoms from the surface of a solid sample in vacuum. The small fraction of sputtered atoms that are ionized form the secondary beam that is drawn into a doubly focusing mass spectrometer where abundances of different species are determined. Sputtering creates a plethora of polyatomic species whose masses may be very similar to those of interest. The SHRIMP RG is well suited to eliminate most of these isobaric interferences by operating at high mass resolution ($M/\Delta M$ = mass/peak width at 10% peak height, in atomic mass units/atomic mass units). At typical run conditions of $M/\Delta M = 7000$, all interferences from otolith material in the 86–88 atomic mass units range, including hydrides, are resolved except for ^{87}Rb, ^{40}Ca^{47}K, and the Ca dimers (e.g., ^{40}Ca^{46}Ca on ^{86}Sr). Here, we present a brief summary of the analytical method. Details, including a complete description of isobaric interferences, are given in Weber et al. (2005).

Analysis of Sr in otoliths was performed with an ~9-nA primary beam of O_2^- focused to a spot ~25 µm × 35 µm. This produced flat bottom craters ~2 µm deep and ~40 counts ^{88}Sr·s^{-1}·ppm^{-1}·nA^{-1}. In a typical analysis of an otolith with ~1000 ppm Sr, this amounts to ~4×10^{-12} g of Sr. Secondary ion intensities at ^{40}Ca^{40}Ca, ^{42}Ca^{40}Ca, ^{85}Rb, ^{86}Sr, ^{87}Sr, ^{88}Sr, and ^{48}Ca^{44}Ca were measured by peak jumping and pulse counting on an electron multiplier. An analysis consisting of 10 cycles through the mass table, including automated peak centering, required 13 min. A correction was made for ^{87}Rb using the ^{85}Rb intensity and ^{85}Rb/^{87}Rb = 2.59265 (Steiger and Jäger 1977). We have found that ^{48}Ca^{39}K does not contribute to counts on ^{87}Sr in otoliths. Data were processed using peak stripping to correct for unresolved isobaric interferences and a working curve defined by reference materials (see below). The working curve yielded results at least as satisfactory as did peak stripping and all data presented here were reduced by that method. The working curve takes into account the different contributions of Ca dimers, assumed to be produced from the common aragonitic matrix in the same proportions, to Sr intensities at 86, 87, and 88 atomic mass units for different Sr/Ca ratios. Analytical routines for Sr isotope analysis traditionally correct for any possible mass-dependent stable (^{84}Sr, ^{86}Sr, and ^{88}Sr) isotope fractionation. A mass fractionation correction was applied based on measured ^{86}Sr/^{88}Sr ratios using a linear law and assuming that ^{86}Sr/^{88}Sr = 0.1194 (Steiger and Jäger 1977).

Reference standards consisted of natural and synthetic calcites and synthetic aragonites. The natural calcites were University of California, Berkeley, museum specimens of a range of Sr concentrations whose ^{87}Sr/^{86}Sr ratios had been

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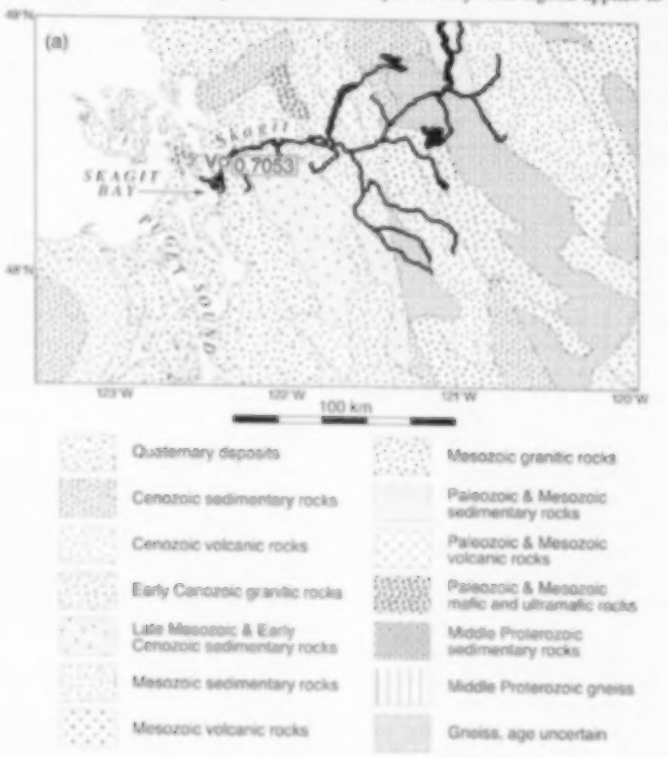
Fig. 3. Fish collection and water sampling sites with generalized geology (after Reed and Bush 2001). (*a*) Skagit River watershed area within the United States and estuary. The number in the box by the sampling site is the $^{87}Sr/^{86}Sr$ ratio of water collected 5 May 2002. (*b*) Central Idaho showing South Fork of the Salmon River, American River – Clearwater River, and Herd Creek – East Fork of the Salmon River. The numbers in boxes by the sampling sites are $^{87}Sr/^{86}Sr$ ratios of water collected in late September 2003. A, American River; S, South Fork Salmon River; H, Herd Creek; V, Skagit River near Mount Vernon; W, Salmon River at White Bird. V and W are USGS National Stream Quality Accounting Network (NASQAN) sites; V also is very close to our Skagit River water sample locality. The legend applies to both maps.



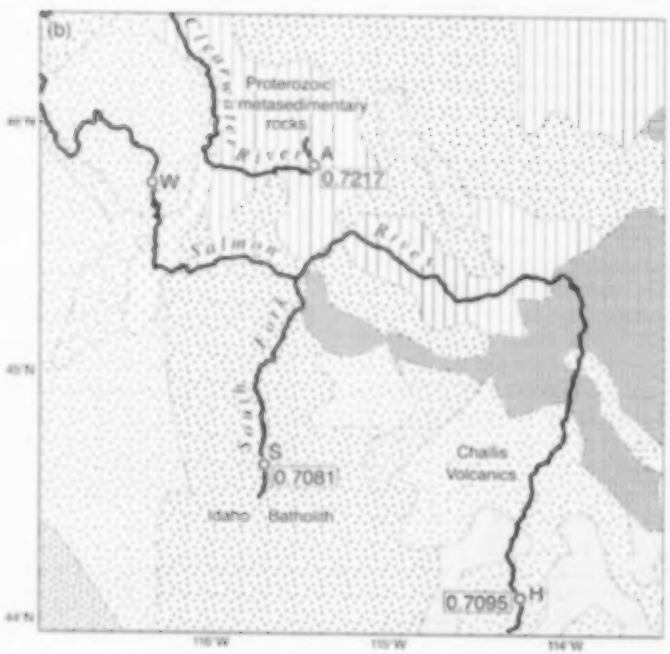


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Table 2. Collection localities and dates, fork lengths, otolith lengths, and radial transect lengths for juvenile Chinook salmon (*Oncorhynchus tshawytscha*).

Specimen	Locality	Collection date	Fork length (mm)	Otolith length (mm)	Transect length (mm)
91-TM-04	Skagit Bay, Washington	17 May 1991	114	2.74	1.07
91-TM-12	Skagit Bay, Washington	17 May 1991	119	2.96	0.79
91-MC-05	Skagit estuary, Washington	15 May 1991	69	1.52	0.60
91-MD-05	Skagit estuary, Washington	17 May 1991	52	1.26	0.50
86-28-08	South Fork Salmon River, Idaho	1 Sept. 1986	56	1.67	0.46
86-01-43	Herd Creek, Idaho	3 Sept. 1986	83	2.57	0.62
86-06-21	American River, Idaho	7 Sept. 1986	57	2.04	0.47

determined by TIMS (Weber et al. 2004). Synthetic carbonates were prepared at high pressure and temperature in the Menlo Park, California, USGS experimental petrology laboratory in a piston–cylinder apparatus. The synthetic materials consisted of calcites made from powders previously analyzed for $^{87}Sr/^{86}Sr$ by TIMS, calcites made from Specpure $CaCO_3$ with a range of amounts of admixed $SrCO_3$ and subsequently analyzed by TIMS, calcite and aragonite made from modern *Tridachna* (EN-1) powder, and calcite and aragonite made from Specpure $CaCO_3$ (~5 ppm Sr). The last of these were used to monitor Ca dimer production. Comparison of $^{87}Sr/^{86}Sr$ ratios measured by the SHRIMP RG on EN-1 composition synthetic calcite and aragonite showed that results for the two matrices were indistinguishable within error limits, indicating that calcite standards can be used for SIMS determination of $^{87}Sr/^{86}Sr$ ratios in aragonitic otoliths.

The external error of an individual $^{87}Sr/^{86}Sr$ analysis was calculated using first-order, second-moment error propagation. The calculation included uncertainty in the $^{87}Sr/^{86}Sr$ measurement and the $^{88}Sr/^{86}Sr$ mass-bias correction, the correlation in these uncertainties, the ^{87}Rb correction to ^{87}Sr, and the uncertainty in the $^{87}Sr/^{86}Sr$ correction from the working curve. Measurement precision is limited by counting statistics calculated based on the total number of counts on ^{87}Sr and ^{86}Sr. During periods of optimal machine performance, calculated external error was ~0.0007 (1σ) per analysis or about twice the uncertainty based on counting statistics alone. During periods of poor machine performance, external error was as large as 0.011, up to four times the uncertainty based on counting statistics. Stability and secondary ion transmission of the SHRIMP RG have been improved significantly since these measurements were made. However, the majority of the data in this paper were collected during periods of suboptimal performance, as can be seen in reported uncertainties (Table D1)[1]. The mean uncertainty of the 134 measurements was 0.0017 and the median was 0.0015. Precision of otolith analyses can be improved by averaging $^{87}Sr/^{86}Sr$ ratios from multiple analysis spots within the same growth increment set. This strategy was employed in choosing points on the otolith samples.

Strontium concentrations were obtained from $^{88}Sr/^{40}Ca^{40}Ca$ ratios by comparison with a subset of the same natural and synthetic calcite reference materials used for determination of $^{87}Sr/^{86}Sr$ ratios and whose Sr concentrations had been determined by solution ICP-MS. Reference to the $^{40}Ca^{40}Ca$ dimer, rather than to Ca monomers (e.g., ^{42}Ca), minimizes the mass range scanned but may introduce error owing to variation in Ca dimer production efficiency between matrices or to sample geometry or surface. Overlap of $^{44}Ca^{44}Ca$ on ^{88}Sr is insignificant in Sr concentration measurement. SIMS data for reference materials and otoliths suggest that uncertainty in Sr concentration owing to variation in Ca dimer production amounts to ≤5% in Sr concentration. This will affect comparison of absolute values of Sr concentration and Sr/Ca ratio between otoliths but probably not within individual otolith transects. Electron microprobe analysis of otoliths 91-MD-05 and 91-TM-12 along radial transects, standardized against calcite and strontianite, yielded Sr/Ca ratios comparable with but less precise than the ion microprobe results.

After the SIMS analyses had been completed, the isotopic composition of Sr in water samples from each of the four fresh water rivers and streams (Table 1) was measured by TIMS at the USGS in Menlo Park, California. Samples were passed through 0.45-μm filters in the field and stored in Nalgene bottles. The samples from Idaho were acidified in the field with HNO_3. Strontium was separated by standard ion-exchange methods and analyzed with a Finnagan MAT 261 mass spectrometer in dynamic mode. Concentrations of Sr and Ca in the filtered samples were determined by ICP-MS in Menlo Park. These data provide a comparison between ambient water and spatially resolved in situ otolith Sr isotopic and concentration information.

Results — fish from four watersheds

Otoliths of juvenile chinook from the Skagit and Idaho watersheds test the ability of SIMS to discriminate between marine conditions that may be inherited maternally and fresh water habitats with $^{87}Sr/^{86}Sr$ ratios notably higher and lower than the well-established marine value of 0.7092. The isotopic data are complemented by simultaneously measured Sr/Ca elemental ratios.

[1] Supplementary data for this article are available on the Web site or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Ottawa, ON K1A 0S2, Canada. DUD 3633. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

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Skagit River and Estuary, Washington

The Skagit River flows west across Phanerozoic sedimentary, igneous, and metamorphic rocks of the North Cascades and continental margin into Skagit Bay (Fig. 3*a*). Rocks in the Skagit drainage have relatively low $^{87}Sr/^{86}Sr$ ratios because they formed in the last few hundred million years near the edge of North America. The 0.70533 ± 2 TIMS $^{87}Sr/^{86}Sr$ ratio (Table 1) of Skagit River water collected in May 2002 (17.6 km from the river mouth and 4.8 km upstream of tidal influence) is consistent with watershed geology. Because this value represents the integrated Skagit drainage, it is possible that water in some tributaries may have significantly higher or lower $^{87}Sr/^{86}Sr$ ratios.

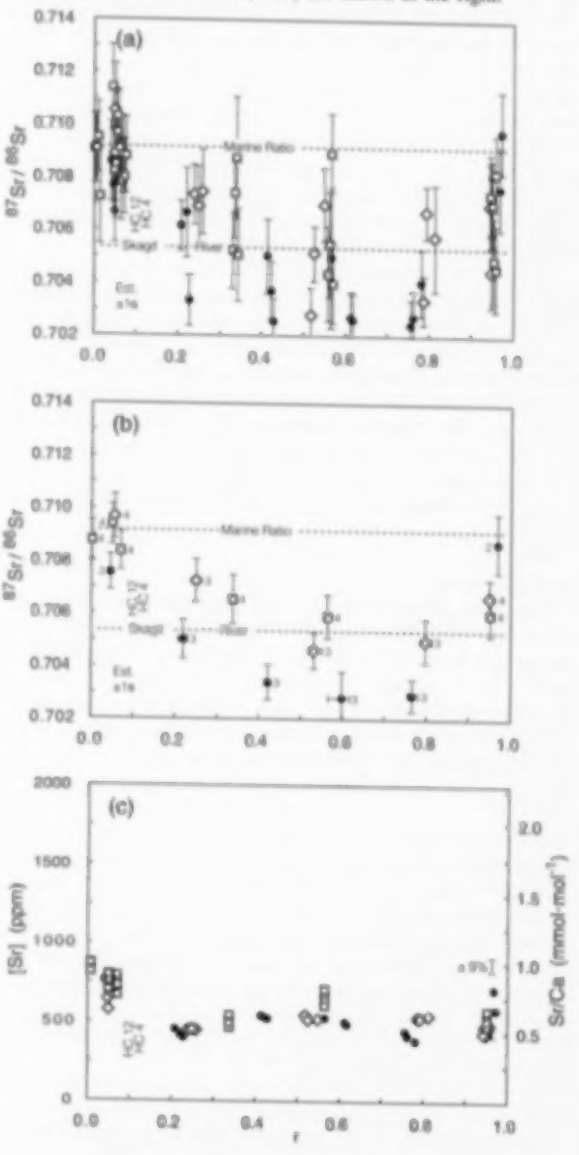
Juvenile salmon were collected in May 1991 from the estuary at the Skagit River mouth and from ~7.4 km away in a shoreline area of Skagit Bay. Skagit ocean-type chinook spend 1–5 years at sea, adults spawn in fresh water in mid-August–October, eggs hatch in winter, fry emerge from February through early April, and juveniles migrate to Puget Sound as early as February or March to as late as September (Skagit System Cooperative and Western Fisheries Research Center 2000).

Skagit Bay

The $^{87}Sr/^{86}Sr$ ratios of otolith prehatch regions in both specimens from Skagit Bay are higher than those of growth increments at 0.2*r*–0.8*r* (Figs. 4*a* and 4*b*) (*r* is the fractional distance from otolith center to edge). The otolith from fish 91-TM-12 has prehatch $^{87}Sr/^{86}Sr$ ratios, inherited maternally, that straddle the marine ratio. Although the $^{87}Sr/^{86}Sr$ ratios are lower, all three prehatch points for fish 91-TM-04 are within 2σ of the marine ratio. It may be that this displacement to lower values reflects systematic error in absolute $^{87}Sr/^{86}Sr$ ratio in this specimen resulting from instrumental factors at the time that these analyses were performed early in the study. The $^{87}Sr/^{86}Sr$ ratios for 0.2*r*–0.8*r* on the otoliths scatter about the 0.70533 ± 2 TIMS value for river water. The low $^{87}Sr/^{86}Sr$ ratios for fish 91-TM-04 at 0.4*r*–0.8*r* may reflect rearing in some tributary of the Skagit River characterized by exceptionally low $^{87}Sr/^{86}Sr$ or may be an analytical artifact caused by an undetected excursion in instrument operating conditions. Both specimens show a return to higher $^{87}Sr/^{86}Sr$ ratios at the most distal set of growth increments analyzed. Note that it was impossible to analyze the outermost parts of some otoliths because of rounding during polishing of specimens that had been mounted on glass slides. The outer points for specimen 91-TM-04 are close to the otolith edge and are within error (1σ) of the marine ratio.

The Sr concentration in the Skagit Bay otoliths ranged from ~400 to ~870 ppm and Sr/Ca ratios from 0.4 to 1.0 mmol·mol^{-1} (Fig. 4*c*). In these otoliths, Sr/Ca ratios appear to discriminate between the marine maternal signal in the prehatch regions and the river signal. However, prehatch and edge Sr/Ca ratios are less than half of the ~2 mmol·mol^{-1} commonly found in otoliths of adult salmonids collected in seawater (e.g., Friedland et al. 1998; Volk et al. 2000). In addition, prehatch and edge Sr/Ca ratios are a maximum of about two times the values for fresh water growth regions, whereas the Sr/Ca ratio of seawater is more than three times that of analyzed Skagit River water (Table 1). Otolith 91-TM-04 shows an increase in Sr/Ca in the outermost points in

Fig. 4. Transects of otoliths from two juvenile chinook salmon from Skagit Bay. Analytical data are plotted against fractional distance from the otolith center (*r*) to the edge to facilitate comparison of results on more than one specimen. Analyses are from a single transect on the otolith from fish 91-TM-04 (circles) and two transects on the otolith from fish 91-TM-12 (squares, transect A; diamonds, transect B) analyzed in different sessions. Each set of four analyses in transect A was obtained at a single location. HC 4 and HC 12 indicate hatch checks in 91-TM-04 and 91-TM-12, respectively. (*a*) $^{87}Sr/^{86}Sr$ ratios. Error bars (external) are ±1σ. (*b*) Weighted mean $^{87}Sr/^{86}Sr$ ratios for analyses of similar sets of growth increments plotted at mean values of *r*. Data were weighted by the inverse of variance of each measurement. Error bars on *r* indicate maximum radial distance between points for which data were averaged. (*c*) Sr concentrations and Sr/Ca ratios. Representative uncertainties (±5%) are shown at the right.



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a similar manner as for $^{87}Sr/^{86}Sr$ ratios (Fig. 4*a*). The relatively low Sr/Ca ratios of the outermost points in otolith 91-TM-12 suggest that the corresponding $^{87}Sr/^{86}Sr$ ratios were lower than the marine value because this portion of the otolith had been deposited before or just as the fish entered salt water. Interpretation of Sr/Ca data for otoliths from all study sites is discussed below.

Skagit estuary

Results for the two fish obtained from Skagit estuary are broadly similar to those for fish collected in Skagit Bay. Again, one fish (91-MC-05) had otolith prehatch and edge $^{87}Sr/^{86}Sr$ ratios that were indistinguishable from the marine ratio (Figs. 5*a*, and 5*b*). Of the two fish from Skagit estuary, this is the one for which data were obtained closest to both the otolith center and edge. Three of the four prehatch $^{87}Sr/^{86}Sr$ ratios from the second fish (91-MD-05) are within 1σ of the marine ratio but the three points near 0.9*r* apparently are not sufficiently close to the edge to have a marine signal and reflect rearing at a site dominated by river water. Data for both fish in the 0.2*r*–0.5*r* region mimic the 0.70533 ± 2 TIMS value for Skagit River water. However, two of the points in the 0.5*r*–0.9*r* part of transect B of the otolith from fish 91-MC-05 overlap the marine ratio but Sr/Ca ratios are similar to other points in this part of the transect, suggesting that these particular isotopic values may be suspect.

The Sr concentrations and Sr/Ca ratios for the two fish from Skagit estuary (Fig. 5*c*) are consistent with marine $^{87}Sr/^{86}Sr$ ratios in prehatch regions and, in specimen 91-MC-05, at ≥0.9*r*. These Sr/Ca values, up to ~1.5 mmol·mol^{-1}, are higher than in comparable regions of otoliths from the two Skagit Bay fish but the values do not approach those expected for full saltwater exposure. The minimum Sr/Ca ratios are similar to those for the Skagit Bay specimens. The low Sr/Ca ratios for specimen 91-MD-05 at ≥0.9*r* are consistent with Skagit River like $^{87}Sr/^{86}Sr$ ratios for the same points.

Idaho streams

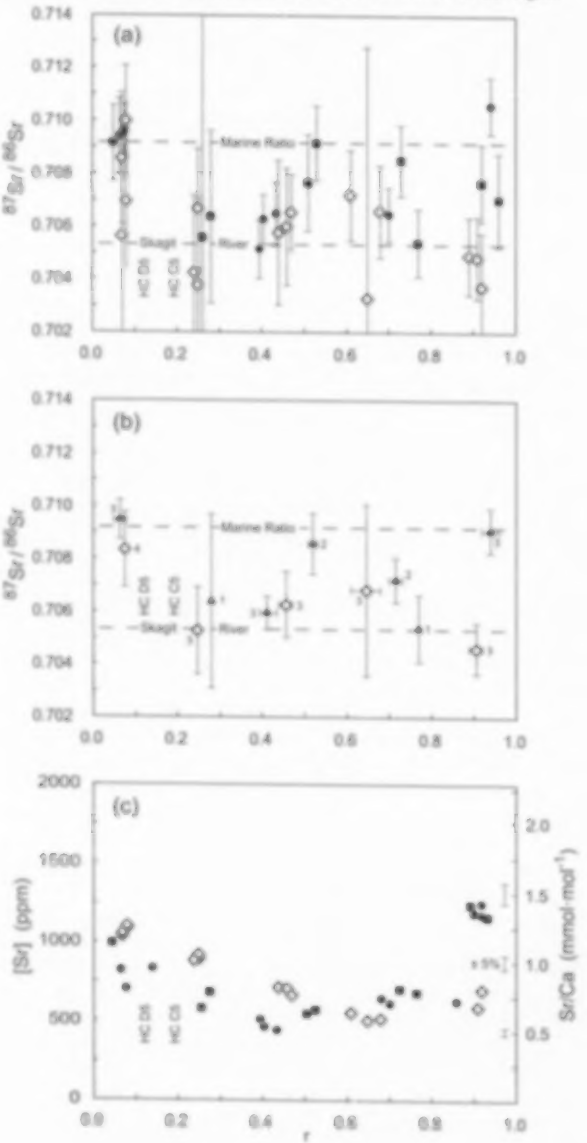
The three Idaho streams drain contrasting geologic terranes. The $^{87}Sr/^{86}Sr$ ratios of the waters vary with the upstream geology of each site. Strontium concentrations in these waters, collected in June–July 2002 and late September 2003, differ between the streams but Sr/Ca ratios are all ~6–8 mmol·mol^{-1} (Table 1). Strontium concentrations in the otoliths studied are higher than in the Skagit River fish, and there is a consistent pattern of radial variation in Sr/Ca ratios.

The stream-type chinook that occur in central Idaho spawn in late August–September, eggs hatch in winter, fry emerge in March–April, and juveniles spend a full year in fresh water before migrating to the sea. Details of life histories of the juvenile chinook collected in September 1986 at the three Idaho sites are unknown. We assume that they hatched and spent their lives upstream or in the vicinity of the collection sites. Their female parents would have journeyed from the Pacific Ocean up the Columbia and Snake rivers to the respective tributaries (Fig. 2).

South Fork of the Salmon River

The South Fork of the Salmon River originates in Cretaceous granitic rocks in the western part of the Idaho Batholith

Fig. 5. Transects of otoliths from two juvenile chinook salmon from Skagit estuary. Analyses are from a single transect on the otolith from fish 91-MD-05 (diamonds) and two transects (circles, transect A; squares, transect B) on the otolith from fish 91-MC-05 analyzed in different sessions (weighted mean values for both transects on 91-MC-05 are plotted as triangles in Fig. *b*). HC C5 and HC D5 indicate hatch checks in 91-MC-05 and 91-MD-05, respectively. (*a*) $^{87}Sr/^{86}Sr$ ratios. Error bars (external) are ±1σ. (*b*) Weighted mean $^{87}Sr/^{86}Sr$ ratios for analyses of similar sets of growth increments plotted at mean values of *r*. Data were weighted by the inverse of variance of each measurement. Error bars on *r* indicate maximum radial distance between points for which data were averaged. (*c*) Sr concentrations and Sr/Ca ratios. Representative uncertainties (±5%) are shown at the right.



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(Fig. 3*a*) where $^{87}Sr/^{86}Sr$ ratios drop off steeply from high values characteristic of the North American craton to low values diagnostic of terranes accreted to the continental margin (Fleck and Criss 1985). The measured TIMS $^{87}Sr/^{86}Sr$ ratios of 0.70802 ± 2 for June 2002 water and 0.70807 ± 2 for September 2003 water from the collection site (Table 1) are virtually identical and are in keeping with the geologic setting.

The South Fork otolith transect began with prehatch $^{87}Sr/^{86}Sr$ ratios of 0.711–0.713, dropped to average values of ~0.709–0.710 in the 0.3*r*–0.6*r* region, and ended with data straddling the river water $^{87}Sr/^{86}Sr$ ratio of 0.708 at 0.7*r*–0.9*r* (Figs. 6*a* and 6*b*). The difference in $^{87}Sr/^{86}Sr$ ratios between 0.3*r*–0.6*r* and 0.7*r*–0.9*r* may indicate migration from the hatch site along unknown tributaries to the reach of the South Fork near the collection site, but precision was insufficient to determine this unequivocally. The maternal signal was nonmarine and high and presumably reflects the female parent's long migration and residence (3–4 months) in Columbia–Snake–Salmon River water during which Sr in her developing eggs lost any isotopic record of a marine history. The high $^{87}Sr/^{86}Sr$ ratio in the prehatch region suggests that a substantial portion of the Sr in the yolk came from the upstream part of this migration path.

The ~1000 to ~1800 ppm Sr concentrations and 1.1–2.0 mmol·mol^{-1} Sr/Ca ratios in the South Fork otolith (Fig. 6*c*) are higher than most of the values recorded for the four Skagit River fish in regions of their otoliths that may reflect marine conditions. The South Fork otolith Sr/Ca ratios approach those measured in otoliths from marine fish. Our June 2002 South Fork water sample has a Sr/Ca ratio notably lower than seawater but the September sample has a Sr/Ca ratio 90% of that of seawater (Table 1). Note that Sr/Ca varies by nearly a factor of 2 along the otolith transect. The Sr/Ca ratio reaches a maximum at ~0.75*r* and drops to intermediate values near the otolith edge. The pattern of Sr/Ca variation is discussed below.

Herd Creek

Herd Creek is a tributary of the East Fork of the Salmon River (Fig. 3*b*). The drainage basin upstream of the collection site is entirely within Eocene Challis Volcanics, rocks derived from continental crust and subcontinental mantle. Present-day $^{87}Sr/^{86}Sr$ ratios in this terrane are likely to be significantly higher than those of the South Fork area because the crustal component in the volcanic magma sources is older and probably has a higher average Rb/Sr ratio. The measured TIMS values of 0.70955 ± 2 and 0.70952 ± 2 (Table 1) for Herd Creek water collected in June 2002 and September 2003 are in harmony with this inference.

The otolith from the stream-type chinook obtained from Herd Creek had prehatch $^{87}Sr/^{86}Sr$ ratios that scattered but averaged ~0.711 (Figs. 7*a* and 7*b*), a Sr isotope signature that presumably reflects the long fresh water journey by the female parent. The $^{87}Sr/^{86}Sr$ ratios for the posthatch transect points were mainly within 1σ and all points analyzed were within 2σ of the Herd Creek water ratio.

Strontium concentrations were ~700–1670 ppm and Sr/Ca ratios were 0.8–1.9 mmol·mol^{-1} for the otolith from the Herd Creek fish (Fig. 7*c*). Overall, values are intermediate between those for fish from the Skagit River and South Fork of the Salmon River, except for prehatch Sr/Ca ratios, which resemble those of the Skagit River fish. As in the South Fork specimen, a Sr concentration and Sr/Ca ratio maximum occur in the Herd Creek fish, but at ~0.5*r* rather than ~0.7*r*.

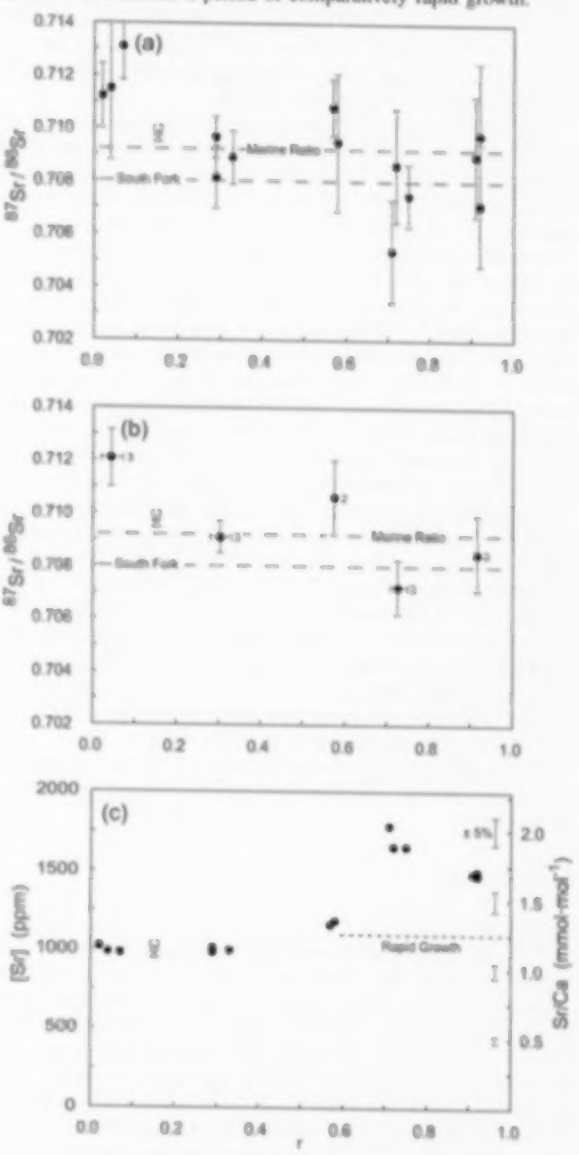

Fig. 6. Transect of an otolith from a juvenile chinook salmon from the South Fork of the Salmon River, Idaho. HC indicates hatch check. (*a*) $^{87}Sr/^{86}Sr$ ratios. Error bars (external) are ±1σ. (*b*) Weighted mean $^{87}Sr/^{86}Sr$ ratios for analyses of similar sets of growth increments plotted at mean values of *r*. Data were weighted by the inverse of variance of each measurement. Error bars on *r* indicate maximum radial distance between points for which data were averaged. (*c*) Sr concentrations and Sr/Ca ratios. Representative uncertainties (±5%) are shown at the right. The broken line indicates a period of comparatively rapid growth.

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American River

The American River is a tributary of the Clearwater River that flows entirely within metamorphosed late Precambrian metasedimentary rocks of the North American craton (Fig. 3*b*). The $^{87}Sr/^{86}Sr$ ratios in this terrane are substantially higher than those of any of the other areas for which otoliths have been analyzed in this study. The TIMS $^{87}Sr/^{86}Sr$ ratio of July 2002 water from the fish collection site is 0.72157 ± 2 and the ratio of September 2003 water is 0.72170 ± 2 (Table 1). Although this is the largest June–July versus September difference in $^{87}Sr/^{86}Sr$ ratios of surface waters in our study area, this result indicates that $^{87}Sr/^{86}Sr$ ratios are unlikely to vary enough in fresh water at any one location to be resolved by SIMS analysis of otoliths.

The $^{87}Sr/^{86}Sr$ ratios along the transect in Figs. 8*a* and 8*b* (note change in scale) were substantially higher than those of any of the other analyzed otoliths. Values for the prehatch region averaged ~0.715 as though the female parent's eggs contained Sr of which some portion, at least, came from the Clearwater–American River system. Values in the intermediate part of the transect are in the 0.717–0.720 range, while four of the six analyses at ≥0.75*r* are indistinguishable from the river water $^{87}Sr/^{86}Sr$ ratio at the collection site (Fig. 8*a*). Although the difference between weighted mean $^{87}Sr/^{86}Sr$ ratios at ~0.2*r*–0.95*r* is insignificant at the 95% confidence level (±2σ), the value at ~0.2*r* is significantly lower than the American River $^{87}Sr/^{86}Sr$ ratio. This suggests that the fish may have migrated to the collection site from a hatch site in some tributary or upstream reach of the American River.

Strontium concentration (~850–2050 ppm) and Sr/Ca data (~1.0–2.5 mmol·mol^{-1}) for the American River otolith (Fig. 8*c*) show a pattern almost identical to that of those for the South Fork specimen (Fig. 6*c*). The two transects differ significantly in the maximum value at ~0.75*r*, but this could result from failure to sample a sharp Sr concentration peak completely in the South Fork or both otoliths. The American River and South Fork specimens provide an example where otolith Sr/Ca ratios are similar because fresh water Sr/Ca ratios are closely comparable in the two streams (Table 1) but $^{87}Sr/^{86}Sr$ ratios of otoliths are markedly different and clearly reflect the isotopic composition of Sr dissolved in ambient river water.

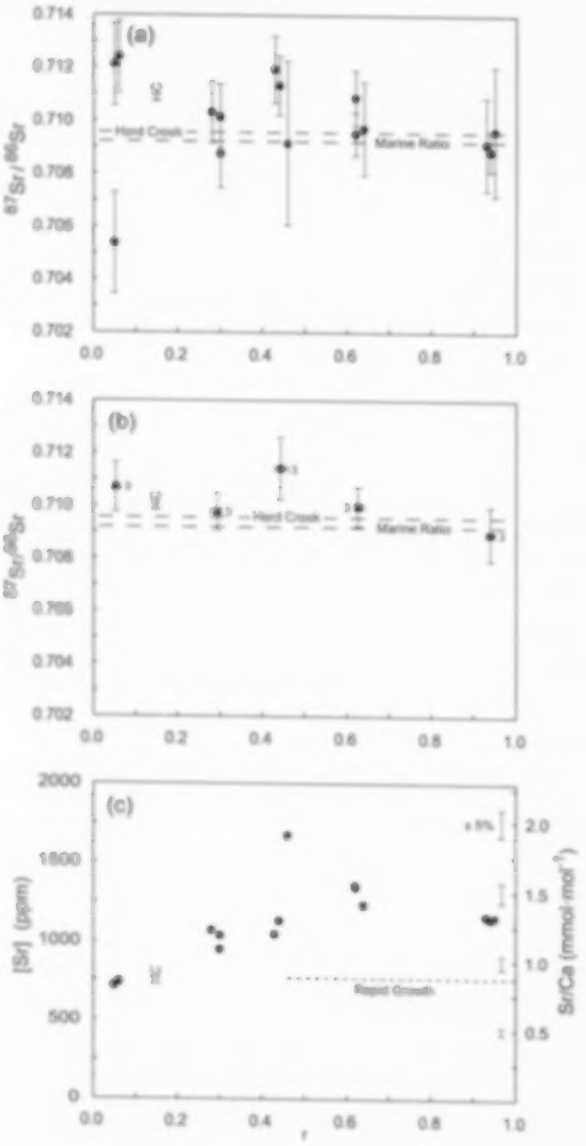
Discussion

Sr isotope ratios

The $^{87}Sr/^{86}Sr$ ratios determined for appropriate sections of otolith transects are consistent with measured river water values within the stated analytical precision. In the Skagit ocean-type chinook, $^{87}Sr/^{86}Sr$ ratios in the prehatch region and near the otolith edge show an unambiguous marine Sr signature. Lack of marine $^{87}Sr/^{86}Sr$ signatures in otolith prehatch regions for the Idaho fish demonstrates the potential for loss of marine Sr in anadromous fish. Finally, we caution that a marine-like $^{87}Sr/^{86}Sr$ ratio in an otolith prehatch region may be acquired from fresh water with $^{87}Sr/^{86}Sr = 0.709$ and it may be impossible to identify anadromous parentage in such cases if the main growth region does not have lower $^{87}Sr/^{86}Sr$ ratios. Such potential ambiguities support use of multiproxy approaches to reconstruct life histories.

It is worth noting that changes in machine operating conditions can significantly perturb the measured $^{87}Sr/^{86}Sr$ ratio and the precision of the corrected $^{87}Sr/^{86}Sr$ ratio. The majority of the analyses in this study were conducted with suboptimal operating conditions, which reduced precision by a factor of 2 relative to optimal conditions. This resulted from

Fig. 7. Transect of an otolith from a juvenile chinook salmon from Herd Creek, Idaho. HC indicates hatch check. (*a*) $^{87}Sr/^{86}Sr$ ratios. Error bars (external) are ±1σ. (*b*) Weighted mean $^{87}Sr/^{86}Sr$ ratios for analyses of similar sets of growth increments plotted at mean values of *r*. Data were weighted by the inverse of variance of each measurement. Error bars on *r* indicate maximum radial distance between points for which data were averaged. (*c*) Sr concentrations and Sr/Ca ratios. Representative uncertainties (±5%) are shown at the right. The broken line indicates a period of comparatively rapid growth.



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our development of the Sr isotope analysis method and collection of the data presented here during the first 3 years of operation of the SHRIMP RG, a prototype instrument. The primary factors associated with reduced measurement precision were high primary beam currents that led to sample charging and to degradation in the uniformity of the Kohler illumination resulting in bowl-shaped or irregular analysis craters. Accuracy was maintained by analyzing standards under the measurement operating conditions.

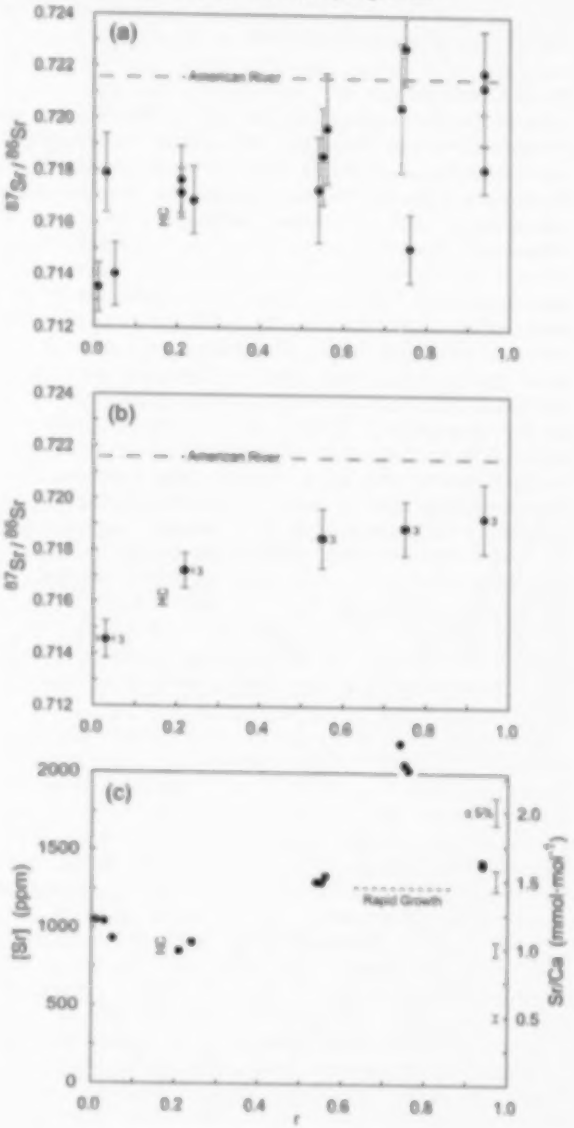
The Sr isotopic data for the Skagit River fish show what is likely the marine signal inherited maternally, the growth of the young fish in the fresh water of the river system, and the time of entry of two of the four juveniles into environments characterized by marine Sr. The Sr isotope measurements discriminate between the potential marine $^{87}Sr/^{86}Sr$ signal and that of the Skagit River when Sr/Ca data show only modest increases relative to fresh water conditions. Conversely, habitat implications of relatively low-precision $^{87}Sr/^{86}Sr$ data for the Skagit estuary fish are corroborated by Sr/Ca ratios indicating continued fresh water residence.

The $^{87}Sr/^{86}Sr$ results for fish from the three Idaho streams reflect surface water chemistry, which is related in a qualitatively predictable way to the geology of the watersheds. Lack of a marine signal in prehatch regions of the otoliths from Idaho fish appears to be a consequence of the female parents' long migration up the Columbia River system to spawning grounds. Alderdice (1988) showed that ion exchange could occur between females and their eggs in the interval prior to spawning. Volk et al. (2000) predicted that spring-migrating chinook that enter river systems with incompletely developed eggs and spend months in fresh water before spawning will have progeny with Sr/Ca ratios in otolith cores that reflect the river water. A corollary is that the $^{87}Sr/^{86}Sr$ ratios of prehatch regions will be diagnostic of river water in systems where the river $^{87}Sr/^{86}Sr$ ratio can be distinguished from the marine $^{87}Sr/^{86}Sr$ ratio, regardless of Sr/Ca ratio, as we have found in our study. The $^{87}Sr/^{86}Sr$ data for the American River specimen hint at a possible difference between maternal and posthatch chemistry that potentially could be related to egg formation in the greater Columbia–Snake–Clearwater River system prior to entry into the part of the upper Clearwater that exclusively drains Precambrian metasedimentary rocks. Near-constancy of $^{87}Sr/^{86}Sr$ ratios along transects in the South Fork and Herd Creek otoliths suggests growth of these fish near the collection sites where TIMS analysis of waters collected in June 2002 and September 2003 shows that $^{87}Sr/^{86}Sr$ ratios are virtually unaffected by seasonal changes in watershed Sr flux. As will be seen below, systematic changes in Sr/Ca ratios are ubiquitous among the Idaho streams of our study.

Sr/Ca ratios

The Sr concentrations and Sr/Ca ratios in the analyzed otoliths differ in magnitude and in radial variation between the Skagit and Idaho fish. We interpret these observations in light of annual cycles in Sr and Ca concentrations and in Sr/Ca ratios evident in USGS water analyses for the Skagit and Idaho drainages as well as potential ambient temperature and somatic growth rate effects. In contrast, Sr isotope ratios of river waters that we analyzed do not appear to be affected by seasonal variation to an extent that can be detected by ion microprobe analysis of otoliths.

Fig. 8. Transect of an otolith from a juvenile chinook salmon from the American River, Idaho. HC indicates hatch check. (*a*) $^{87}Sr/^{86}Sr$ ratios. Error bars (external) are ±1σ. (*b*) Weighted mean $^{87}Sr/^{86}Sr$ ratios for analyses of similar sets of growth increments plotted at mean values of *r*. Data were weighted by the inverse of variance of each measurement. Error bars on *r* indicate maximum radial distance between points for which data were averaged. (*c*) Sr concentrations and Sr/Ca ratios. Representative uncertainties (±5%) are shown at the right. The broken line indicates a period of comparatively rapid growth.



Water analyses

The Sr/Ca ratios measured on the otoliths may be compared with the data for waters that we sampled and also with dissolved Sr and Ca analyses from the USGS National Stream

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Quality Accounting Network (NASQAN) (http://water.usgs.gov/nasqan). The NASQAN samples typically were collected four times per year during November 1982 through September 1993 at (*i*) the Skagit River near Mount Vernon, Washington (site 12200500, drainage area 8011 km^2), just downstream from our 2002 water sample, (*ii*) the Clearwater River at Spalding, Idaho (site 13342500, drainage area 24 786 km^2), near its confluence with the Snake, and (*iii*) the Salmon River at White Bird, Idaho (site 13317000, drainage area 35 094 km^2), also near its confluence with the Snake. The NASQAN data (Fig. 9) include the years in which our chinook specimens were obtained.

Skagit River chinook

The otolith Sr/Ca ratios complement the $^{87}Sr/^{86}Sr$ data for fish from the Skagit River. The Sr/Ca ratios provide a fresh water – salt water habitation indicator in this case because Skagit River water has Sr/Ca ratios less than one third of the marine value. Therefore, where otolith $^{87}Sr/^{86}Sr$ cannot be differentiated from the marine ratio, low otolith Sr/Ca ratios can be used to confirm fresh water habitation. Where otolith Sr/Ca is elevated, $^{87}Sr/^{86}Sr$ can be used to check for the possibility of a marine source. The Sr/Ca ratios near otolith edges are lower than commonly reported for salmonids living in marine water, suggesting that these fish were recent migrants to the sampling locations. The prehatch Sr/Ca ratios are consistent with Rieman et al. (1994) who found that Sr/Ca ratios in otolith primordia of sockeye salmon (*Oncorhynchus nerka*) were lower than for outer portions of the same otoliths that grew in marine conditions. Relatively low Sr/Ca ratios measured near otolith edges for Skagit Bay and one Skagit estuary juvenile suggest that we did not analyze sufficiently close to the actual edges to sample material that was deposited during exposure to undiluted seawater. However, the outermost $^{87}Sr/^{86}Sr$ ratio for the Skagit Bay specimen that was analyzed closest to its edge is indistinguishable from the marine ratio, as one would expect for ambient water that was a mixture of fresh and salt water.

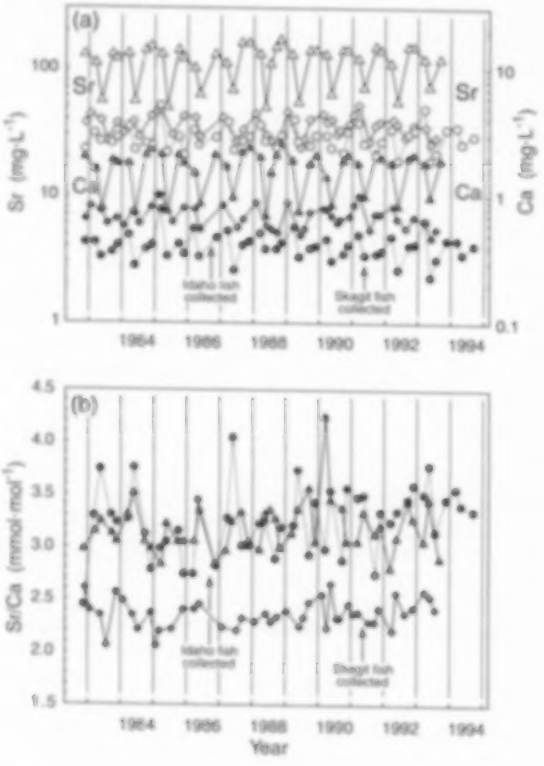
Partitioning of Sr and Ca between environmental water and a growing otolith can be expressed as a partition coefficient, $D_{Sr} = [Sr/Ca]_{otolith}/[Sr/Ca]_{water}$, keeping in mind that the path between ambient water and otolith is complex and may be affected by physiological factors (Campana 1999). Although NASQAN Sr and Ca concentrations in the Skagit River varied systematically with season (Fig. 9*a*), fluctuation in the Sr/Ca ratio was irregular (mean 2.36 ± 0.13 (1σ) mmol·mol^{-1}, indistinguishable from our analysis of 2002 water). The Skagit River Sr/Ca ratio (Fig. 9*b*) was effectively constant during the year that chinook were collected for our study (1991). This is consistent with our Sr/Ca analyses of otoliths from Skagit Bay and estuary fish that had approximately constant Sr/Ca ratios during fresh water growth. The fresh water growth zones of the Skagit otoliths therefore suggest a D_{Sr} of ~0.25, a value similar to those implied by other studies of chinook salmon (e.g., Zimmerman et al. 2003), that can be used to interpret variation in Sr/Ca ratios in the other chinook otolith specimens.

Idaho chinook

Analyzed Sr concentrations and Sr/Ca ratios in the otoliths from Idaho stream-type chinook typically are higher than in prehatch regions or near edges of otoliths from the Skagit ocean-type chinook. The pattern displayed by Sr/Ca ratios in the Idaho otoliths, in which Sr/Ca ratios have a maximum value at 0.5*r*–0.8*r* and an intermediate value near the otolith edge in spite of virtually constant posthatch $^{87}Sr/^{86}Sr$ ratios, points to a common mechanism. The observed variation in otolith Sr/Ca ratios may result from multiple factors, including seasonal variation in ambient water Sr/Ca ratio and (or) temperature and physiological effects on elemental discrimination.

The peaks in Sr/Ca ratios in the Idaho fish collected in early September correspond to spring or summer of 1986. Counts of diel growth increments inward from otolith edges indicate that the Sr/Ca peaks were not synchronous for the different fish. Maximum otolith Sr/Ca ratios occurred near the end of April in the fish from Herd Creek, near the end of June in the American River, and in mid-July in the South Fork of the Salmon River. If ambient water Sr/Ca ratio can be calculated from otolith Sr/Ca values for the posthatch pe-

Fig. 9. Seasonal variation in dissolved Sr and Ca in the Skagit (diamonds), Salmon (triangles), and Clearwater (circles) rivers (USGS National Stream Quality Accounting Network (NASQAN) data for sites 12200500, 13317000, and 13342500, respectively; http://water.usgs.gov/nasqan). See Figs. 2 and 3 for locations of sampling sites. Reported 8 May 1986 Clearwater River Sr value appears to be in error; plotted value estimated on the basis of Ca concentrations and Sr/Ca ratios for May Clearwater samples collected in other years. (*a*) Sr concentrations (open symbols) and Ca concentrations (solid symbols). (*b*) Sr/Ca ratios.



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riod using D_{Sr} = 0.25, spring–summer Sr/Ca ranges for these streams were 4.3–7.6, 3.9–10, and 4.5–8.1 mmol·mol^{-1}, respectively. Our analyses of waters collected from the same localities in June–July 2002 and September 2003 yielded Sr/Ca ratios of 5.8–8.1 mmol·mol^{-1}, within the spring–summer 1986 range implied by the otolith ratios. This suggests that the pattern of Sr/Ca variation along otolith transects results from secular changes in ambient water Sr/Ca ratios.

The NASQAN data for the two Idaho sites display large seasonal fluctuations in Sr and Ca concentrations, greater for the Salmon and less for the Clearwater (Fig. 9*a*). Although concentrations were lowest, Sr/Ca ratios (Fig. 9*b*) typically were highest during spring runoff (represented by May samples). The Clearwater River had Sr concentrations comparable with the Skagit but had a Sr/Ca ratio that ranged from ~2.4 to ~4.0 mmol·mol^{-1} (excluding a reported 8 May 1986 value of 11.8 that appears incorrect because of anomalous Sr concentration). The Salmon River had Sr concentrations roughly three times those of the Skagit, varying seasonally in a consistent manner by a factor of 2. The Salmon had Sr/Ca ratios ranging from ~2.8 to 4.2 mmol·mol^{-1} and, as with the Clearwater, tended to show maximum Sr/Ca values in spring and minimum values in winter, including 1986 when our chinook were collected. The June–July 2002 Sr/Ca ratios of 5.8–6.3 mmol·mol^{-1} and September 2003 Sr/Ca ratios of 6.4–8.1 mmol·mol^{-1} for the streams in our study are notably higher than any of the 1982–1993 NASQAN values for the Clearwater and Salmon rivers farther downstream (recall that our 2002 Skagit River water analysis agrees with NASQAN data from virtually the same site). Although both Idaho NASQAN sites are far downstream from our collection localities, and thus sample large drainages with heterogeneous geology, the seasonal variation in Sr/Ca ratio is similar in relative magnitude and timing to, and appears to be approximately in phase with, the radial Sr/Ca variation in the analyzed otoliths. Our own data for waters from the fish collection sites vary in the same sense between June–July 2002 and late September 2003. This suggests that, at least to a first approximation, the observed Sr/Ca variation along otolith transects reflects seasonal cycles in geochemical processes common to the three watersheds.

Studies of temperature effects on Sr/Ca partitioning between otoliths and environmental water have yielded inconsistent results and suggest little (Bath et al. 2000) or no significant temperature dependence (Tzeng 1994; Kawakami et al. 1998). In any case, it is highly unlikely that temperature variation could account for all of the observed twofold radial change in otolith Sr/Ca ratios (Campana 1999).

A plausible supplementary explanation for the pattern of Sr/Ca variation in the otoliths from the stream-type chinook from Idaho is that increases in Sr/Ca ratios correspond to times of stress and (or) decreased somatic growth rate (e.g., Sadovy and Severin 1994; Friedland et al. 1998; Campana 1999). Campana (1999) proposed that a crystallization process in which otolith Sr/Ca ratio is inversely proportional to matrix protein formation rate would explain observations of presumed temperature and growth rate effects on otolith Sr/Ca ratios. He suggested that both Sr/Ca ratios and their temperature dependence should be highest in otoliths with low protein synthesis (growth) rates and this would explain a peak in Sr/Ca ratio at metamorphosis from the larval stage because this is a time of diminished growth. Any temperature effect on otolith Sr/Ca ratios probably would covary with growth rate effects (Friedland et al. 1998). Increase in Sr/Ca ratio with decreasing growth rate, however, does not explain the observed variation in Sr/Ca ratio in the otoliths from Idaho fish because the Sr/Ca maxima occur in regions with relatively wide diel growth increments, i.e., periods of comparatively rapid growth.

The basic interpretation of the otolith Sr/Ca elemental ratio data is that different radial variation patterns in Sr/Ca ratios in otoliths from the Skagit drainage and from central Idaho reflect contrasts in watershed geology and in seasonal ambient water Sr/Ca fluctuation. The data for these samples suggest that somatic growth rate and temperature influences on D_{Sr} are less important. In the face of ambiguities in interpreting Sr/Ca ratios, combination of the concentration and isotopic data provides a powerful tool for monitoring changes in fishes' geographic location between the ocean and specific watersheds and also in factors affecting otolith Sr/Ca ratios.

In conclusion, in situ analysis of Sr isotopic composition by SIMS using a high-transmission, high mass resolution ion microprobe can provide otolith $^{87}Sr/^{86}Sr$ data on a scale relevant to otolith growth increment banding. These data can be used to infer geochemical properties of ambient waters and thus to help determine natal streams and track migration and rearing histories of salmonids. The spatial resolution and shallow depth penetration of the ion microprobe enable repeated isotopic analysis of otolith prehatch regions, and even individual primordia, that may be impossible by other methods such as micromilling or LA-ICP-MS.

Results for transects on otoliths of wild juvenile chinook salmon from four drainages with distinctive geology and fresh water Sr isotopic compositions demonstrate how the method can be applied to distinguish migration and rearing histories. Otoliths of outmigrating juvenile ocean-type chinook from the Skagit River, which traverses the comparatively low $^{87}Sr/^{86}Sr$ Cascades Range of Washington, retain a marine-like signal in prehatch regions, show a low $^{87}Sr/^{86}Sr$ ratio similar to that of Skagit River water across their fresh water growth histories, and display a return to marine influence prior to capture in the Skagit Bay or estuary. In contrast, otoliths of wild juvenile stream-type chinook collected in three watersheds in central Idaho have prehatch $^{87}Sr/^{86}Sr$ ratios that exceed the marine ratio and posthatch ratios that are close to the Sr isotopic compositions of water from the collection sites. The prehatch Sr isotopic compositions of otoliths from Idaho juveniles appear to reflect exchange or incorporation of Sr in developing eggs during the female parents' long migration and residence in fresh water prior to spawning. This result confirms previous work suggesting that the progeny of stream-type chinook may not inherit a marine Sr signal.

The Sr/Ca and $^{87}Sr/^{86}Sr$ ratios are complementary in differentiating between the marine and fresh water Sr signals. In the case of the Skagit drainage, where fresh water Sr/Ca ratios are significantly lower than marine values, Sr/Ca can be used to confirm the marine prehatch $^{87}Sr/^{86}Sr$ ratio. For the Idaho streams, the high prehatch Sr/Ca signal can be in-

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terpreted as nonmarine because of the nonmarine $^{87}Sr/^{86}Sr$ ratios at those same locations in the otoliths. In the case of ocean-type chinook from natal streams with marine-like fresh water $^{87}Sr/^{86}Sr$ ratios, one that we have not studied, elemental Sr/Ca ratios of otoliths may discriminate between marine and fresh water growth as long as the Sr/Ca ratio of fresh water is substantially different from that of seawater.

The Sr/Ca and $^{87}Sr/^{86}Sr$ ratios also are complementary in identifying natal location and fresh water rearing history. Our data demonstrate that otolith Sr/Ca does reflect differences in fresh water Sr/Ca and may complement $^{87}Sr/^{86}Sr$ in some cases. However, in the case of the central Idaho streams, interpretation of Sr/Ca ratios along otolith transects as reflecting different habitats is ambiguous because of a radial pattern in Sr/Ca variation that is common to all three Idaho study sites. The Sr/Ca ratios in the Idaho otoliths apparently reflect major seasonal (and annual) fluctuation in ambient water Sr/Ca ratios that does not appear to exist for Sr isotopic composition. Together, the isotopic and elemental concentration data strongly support multiproxy approaches to reconstruct life history from ambient water geochemistry.

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Tailoring palaeolimnological diatom-based transfer functions

Julien M.J. Racca, Irene Gregory-Eaves, Reinhard Pienitz, and Yves T. Prairie

Abstract: This paper presents a method designed to build species-tailored diatom–environment models. Using a pruning algorithm of artificial neural networks, powerful species-tailored models constrained to water temperature, water depth, and dissolved organic carbon were developed from a 109-lake training set from northwestern Canada and Alaska. The reasoning behind the approach is that the implementation of a single, gradient-based, organism–environment relationship should only use species that are comprehensively influenced by the variable of interest. By pruning species according to their relevance to each of the three studied variables, the cross-validated performances of all three models were significantly increased, suggesting that nonrelevant species have corrupting influences and need to be removed. The removal of corrupting species also suggests that palaeolimnological transfer functions based on an appropriate subset of useful species are more independent.

Résumé : Nous présentons une méthode pour construire des modèles diatomées–environnement basés sur les espèces. À l'aide d'un algorithme d'élagage tiré des réseaux neuraux artificiels, nous avons mis au point des modèles basés sur les espèces avec une contrainte pour la température de l'eau, la profondeur et la concentration de carbone organique dissous à partir d'une série expérimentale de données sur 109 lacs du nord-ouest canadien et de l'Alaska. Le raisonnement qui sous-tend la méthode est que l'établissement d'une relation particulière organisme–environnement basée sur un gradient ne devrait utiliser que des espèces qui sont influencées de façon globale par la variable considérée. Par l'élagage des espèces d'après leur pertinence vis-à-vis chacune des trois variables étudiées, les performances des trois modèles déterminées par validation croisée sont significativement améliorées, ce qui indique que les espèces non pertinentes ont une influence nuisible et doivent être retirées. Le retrait des espèces nuisibles indique aussi que les fonctions de transfert paléolimnologiques basées sur un sous-ensemble approprié d'espèces utiles sont plus indépendantes.

[Traduit par la Rédaction]

Introduction

Transfer functions that quantify the modern relationships between the composition of diatom assemblages and environmental variables for a set of lakes are routinely used in palaeolimnological studies to infer quantitative environmental changes from past diatom assemblage data. Several methods, based on different algorithm types, have been successfully applied to model the complex relationships between taxon assemblages and environmental variables: weighted averaging regression – calibration based approach (ter Braak and van Dam 1989; Birks et al. 1990), weighted averaging partial least-squares regression (ter Braak and Juggins 1993), maximum likelihood based approach (ter Braak and van Dam 1989; ter Braak et al. 1993), full probability based approach (Bayesian modeling) (Ellison 1996; Toivonen et al. 2001; Vasko et al. 2000), and artificial neural networks based approach (Racca et al. 2001; Köster et al. 2004).

While it is clear that the predictive ability of any of these methods depends ultimately on the degree to which the distribution of the biota assemblages is actually determined by environmental characteristics, it is also affected by the sampling characteristics of the modern data set (distributions and ranges of the environmental variables, number of samples, number of taxa, amount of noise, etc.) (Racca and Prairie 2004). Because relationships between the composition of species assemblages and environmental variables are extracted from a restricted set of lakes, the predictive ability of a particular model is necessarily dependent on the choice of lakes included in the training set. In general, modern training sets are designed either to be as encompassing as possible or to focus on a predetermined environmental gradient. Thus, depending on the subsequent use of a model, lakes in a training set are first chosen to cover a large range of the environmental variable of interest but also to cover a small range of other variables. With such a design, it is expected

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J.M.J. Racca[1] and R. Pienitz. Paleolimnology–Paleoecology Laboratory, Centre d'Études Nordiques et Département de Géographie, Université Laval, Québec, QC G1K 7P4, Canada.
I. Gregory-Eaves. Department of Biology, University of Ottawa, 150 Louis Pasteur Street, Ottawa, ON K1N 6N5, Canada.
Y.T. Prairie. Département des Sciences Biologiques, Université du Québec à Montréal, Case postale 8888 succ. Centre-Ville, Montréal, QC H3C 3P8, Canada.

[1]Corresponding author (e-mail: racca.julien@courrier.uqam.ca).

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that the variation in assemblage data will be attributed principally to the changes in the environmental variable of interest. Also, it is expected that the effects of other variables will have little impact on the variation in the assemblage data. As a result, diatom transfer functions based on such optimal training sets generally exhibit good predictive power (e.g., Fallu and Pienitz 1999), whereas models based on more limnologically diverse lakes, where variation in species assemblages can be influenced by several environmental gradients, exhibit generally lower predictive power (e.g., Philibert and Prairie 2002).

In this study, we suggest that much more powerful models can be developed from a less optimal training set design. Here, we apply a method to build optimal subtraining sets from an existing nonoptimal full training set. In contrast with the aforementioned design where the training set is constructed based on a choice of lakes, the proposed method deals with the selection of taxa according to their relative contribution in a model. We hypothesize that most of the complexity in a training set, which can be attributed either to the effect of the multiple environmental influences on assemblage data in limnologically diverse lakes or to stochastic variability within the data set, could be better constrained if only species whose distribution is comprehensively dependent on the variable being studied are included in a training set.

To test this idea, we developed three diatom-based training sets constrained to (*i*) water temperature, (*ii*) water depth, and (*iii*) dissolved organic carbon (DOC) from an original training set where the lakes spanned a wide range in all of these three gradients resulting from the combination of two diatom-training sets from northwestern Canada and Alaska (Pienitz et al. 1995; Gregory-Eaves et al. 1999). The main objective of the study was to show that the predictive ability of a model can be increased when it is species tailored to a particular variable (i.e., when only the subset of species whose distribution and abundance are comprehensively related to the environmental variable is used).

Materials and methods

Study area

The extended modern training set of 109 lakes used in this study results from the combination of a 58-lake training set from the Yukon and the Northwest Territories (Pienitz et al. 1995) and a 51-lake training set from Alaska (Gregory-Eaves et al. 1999) (Fig. 1). The 58 lakes from the Yukon and the Northwest Territories are located between Whitehorse and Tuktoyaktuk ranging from 60°37′N to 69°35′N and from 132°04′W to 138°22′W. The locations of the 51 Alaskan lakes range from 60°28′N to 69°35′N and from 141°38′W to 150°49′W. Details of the limnological, physiographic, and geological features for each training set are reported in Pienitz et al. (1995, 1997) and Gregory-Eaves et al. (1999). The lakes of each training set were chosen to span a broad north–south climatic gradient, but by combining the two sets, a fairly large east–west gradient is also captured. Combining the two data sets enlarges the ranges of several limnologically and nonlimnologically associated variables. We summarize the ranges covered by lake-related variables for the 109 training set sites in Table 1.

Sample collection

Sample collection in the field and measurements of related environmental variables (water temperature, water depth, pH, conductivity, and water transparency) were done in the summers of 1990 and 1996 for the Yukon and Alaskan training sets, respectively. Laboratory analyses of nutrients, major ions, and trace metals were performed by the National Water Research Institute (Burlington, Ontario) following standard methods. Full details of field sampling methods, water chemistry, and other analyses are provided in Pienitz et al. (1995, 1997) and Gregory-Eaves et al. (1999, 2000).

Diatom slides were prepared by treating surface sediment samples of each site using standard methods (Pienitz et al. 1995). Identification and enumeration of diatom valves were done along random transects under oil immersion using light microscopy. For each slide, between 300 and 500 diatom valves were identified to the lowest taxonomic level using primarily the following taxonomic sources: Krammer and Lange-Bertalot (1986–1991), Foged (1981), Patrick and Reimer (1966, 1975), Cumming et al. (1995), Camburn et al. (1984–1986), and Fallu et al. (2000). The harmonization of species identification between the two training sets was made on multiple occasions during several diatom taxonomic workshops (e.g., Arctic and Antarctic Diatom Workshop (5th), 1995, unpublished report, Queen's University, Kingston, Ontario). A total of 545 diatom species were identified in the 109 surface samples but only 259, with a relative abundance of 1% in at least three samples, were used for the analyses. Details regarding these species can be found in Appendix A.

Numerical analyses

Artificial neural networks transfer functions

Although the ecological response curve of all species in regard to one environmental gradient is often assumed to be unimodal, a mixture of different response curves is often observed in palaeolimnological training data sets (e.g., unimodal, skewed unimodal, sigmoidal increasing, or sigmoidal decreasing) (Birks 1998). We used artificial neural networks to implement the transfer functions because artificial neural networks are capable of accommodating the full range of species response curves (Leshno et al. 1993). So-called multilayer perceptrons, one type of network architecture trained with a back-propagation algorithm (Rumelhart et al. 1986), have been successfully applied in quantitative palaeolimnology (Racca et al. 2001; Philibert et al. 2003; Köster et al. 2004) and palaeoceanography (Malmgren and Nordlund 1997; Peyron and De Vernal 2001). Here, the same network architecture is used. In this type of network, neurons are arranged in a distinct layered topology: one input layer (representing independent variables (species)), one hidden layer, and one output layer (representing dependent variables (environmental variables)). All neurons from one layer are connected to all neurons in the adjacent layers and all of these connections have a weight that represents the parameters of the network. By back-propagation (iterative process), the weights of the connections are adjusted by feeding a set of input–output pattern pairs many times. As a result of these weight adjustments, internal hidden neurons, which are not part of the input or output, come to represent important

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Fig. 1. Map of study sites showing the position of the 51 Alaskan and 58 Yukon calibration lakes. Inset shows the location in North America.

features of the task domain and the relationship between input and output is captured by the interactions of these units. This relationship (function) can then be used to predict new output (i.e., values of environmental variables) from new input data (i.e., species assemblages). Background information on neural networks is available in various introductory textbooks such as Bishop (1995) and more details of this methodology as applied to palaeolimnology can be found in Racca et al. (2001).

Building constrained training set based transfer functions

To build optimal subtraining sets, we used the skeletonization pruning algorithm of artificial neural networks (Moser and Smolensky 1989). Pruning algorithms (e.g., Reed 1993) are comparable with backward elimination in regression models. Backward elimination starts with all independent variables and sequentially removes the least relevant one and stops if the model performance drops below a given threshold by the removal of any of the remaining independent variables. The skeletonization algorithm was already applied to estimate the functionality of individual species in the Surface Water Acidification Program training data set (Birks et al. 1990) with the objective of removing nonrelevant and redundant species from a pH model (Racca et al. 2003). Using skeletonization, the relevance of one species (i.e., its relative contribution) is determined as an estimation of the change in the model error (i.e., root mean square error, RMSE) when this species is omitted: the more the model error increases, the more a species is relevant and vice versa. The estimated relevance can, therefore, be viewed as a direct measure of the numerical importance of each species in the model and can be used to remove species according to their relative contribution.

Here, we used the skeletonization method to prune diatoms according to their contribution to water temperature, water depth, and DOC. Pruning routines were applied until optimal constrained sets of species were reached. This involves consecutive and alternative steps of training–pruning simulation, as skeletonization pruning is a dynamic procedure. Details of the skeletonization–pruning algorithm used in this study can be found in Racca et al. (2003).

Pruning procedures and model validation

The same pruning parameter setup was applied to each simulation: from the initial full data set, noncontributing species were removed (one by one) according to their numerical importance until the removal of one species increased the model error over a fixed criterion. For each training–pruning simulation, species removal begins when the model has converged (i.e., when the error remains quasi-

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Table 1. Summary of the ranges of environmental variables for both training sets and for the combined training set.

	Yukon training set					Alaska training set					Combined training set				
	Min.	Max.	Mean	Median	SD	Min.	Max.	Mean	Median	SD	Min.	Max.	Mean	Median	SD
ALT (m)	15.0	1387.0	361.6	122.0	393.0	35.0	1028.7	429.4	320.0	322.1	15.0	1387.0	393.4	251.5	361.5
DEPTH (m)	1.0	49.0	7.4	4.0	8.4	0.8	54.0	10.5	5.0	12.1	0.8	54.0	8.8	5.0	10.3
pH (unity)	5.9	9.3	7.9	8.1	0.6	7.0	9.3	7.9	7.9	0.5	5.9	9.3	7.9	8.0	0.6
TEMP (°C)	12.0	23.0	18.2	18.0	2.3	9.8	22.9	15.5	16.1	3.0	9.8	23.0	16.9	17.0	2.9
COND ($\mu S \cdot cm^{-1}$)	24.0	1500.0	160.7	112.0	212.4	6.0	434.0	100.7	82.0	89.0	6.0	1500.0	132.7	94.0	168.4
TPU ($\mu g \cdot L^{-1}$)	3.0	55.1	15.6	12.3	11.8	1.3	475.8	24.9	11.2	66.3	1.3	475.8	20.0	11.4	46.1
DOC ($mg \cdot L^{-1}$)	3.1	35.1	12.3	10.8	6.5	2.7	257.0	66.5	44.4	68.5	2.7	257.0	37.7	14.2	54.1
DIC ($mg \cdot L^{-1}$)	0.3	134.2	17.9	13.1	22.1	1.1	59.5	13.6	12.0	11.3	0.3	134.2	15.9	12.1	17.9
TKN ($\mu g \cdot L^{-1}$)	72.0	1293.0	440.8	368.0	247.5	50.0	2400.0	511.4	346.0	479.0	50.0	2400.0	473.8	352.0	373.9
SiO_2 ($mg \cdot L^{-1}$)	0.1	12.5	2.2	1.0	2.9	0.1	10.8	2.2	1.2	2.8	0.1	12.5	2.2	1.0	2.8
SO_4 ($mg \cdot L^{-1}$)	0.5	1242.0	41.3	8.9	165.8	0.2	43.1	7.3	5.1	9.2	0.2	1242.0	25.4	6.0	121.8
Ca ($mg \cdot L^{-1}$)	3.5	50.3	19.6	18.6	12.0	0.3	50.0	14.4	13.2	11.9	0.3	50.3	17.2	15.4	12.2
Na ($mg \cdot L^{-1}$)	0.2	187.0	8.9	3.9	25.0	0.2	11.6	1.9	1.0	2.3	0.2	187.0	5.6	2.1	18.6
K ($mg \cdot L^{-1}$)	0.1	29.9	1.9	1.2	4.0	0.2	15.6	1.1	0.6	2.2	0.1	29.9	1.5	1.0	3.3
Cl ($mg \cdot L^{-1}$)	0.2	75.2	7.3	2.0	13.4	0.1	6.0	1.4	1.1	1.2	0.1	75.2	4.5	1.5	10.2
Fe ($\mu g \cdot L^{-1}$)	5.9	1660.0	213.3	86.6	318.4	10.0	1920.0	180.2	57.0	370.0	5.9	1920.0	197.8	72.0	342.3
Mn ($\mu g \cdot L^{-1}$)	2.0	160.0	23.7	15.0	29.7	1.0	58.7	12.7	8.8	12.4	1.0	160.0	18.5	12.0	23.8

Note: ALT, altitude; DEPTH, water depth; TEMP, water temperature; COND, conductivity; TPU, total phosphorus unfiltered; DOC, dissolved organic carbon; DIC, dissolved inorganic carbon; TKN, total Kjeldahl nitrogen.

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constant even after iterations are added) and species removal is stopped when the error increases by 10% over the error at the starting point of pruning. This procedure was repeated as long as the training–pruning simulations were possible (i.e., a new training–pruning simulation was applied to reduced data sets until no retraining iteration after a species deletion could lower the error below the threshold necessary to end pruning). We kept this threshold quite low (10% over the RMSE at the starting point) so as to ensure that the removal steps were small (i.e., where few species are removed at each step instead of only one or two training–pruning simulations where many species are removed). Moreover, the number of iterations for the retraining phase of each training–pruning simulation was kept low (20) for the same reason (i.e., the longer is the retraining phase, the better the model error converges and more species are removed at each training–pruning simulation). Although several pruning parameter configurations could be used, our experience is that the order of species removal is not dramatically changed. Ultimately, only the number of pruned species can be modified by the pruning parameter configuration. The pruning procedures were performed using Stuttgart Neural Network Simulator v4.2 (Zell et al. 1996).

However, because skeletonization pruning of species is based on the change of the apparent error function (i.e., apparent RMSE), a validation of the pruned model was made using a standard back-propagation model with cross-validation based on leave-one-out jackknifing. It is this cross-validated error term that we ultimately seek to improve by tailoring the transfer function (i.e., by pruning out the species judged irrelevant for the particular variable modeled). For this purpose, the same methodology as proposed in Racca et al. (2001, 2003) was applied using a cross-validation routine (CROSVAL) (R. Racca, Département des Sciences, Université de Nouvelle Calédonie, BP 4477, 98847 Noumea CEDEX, Nouvelle-Calédonie, unpublished program) of YANNS (Bosé et al. 1998).

Results

Data set characteristics

Because of the strong latitudinal gradient covered by both training sets, several distinctive changes in diatom assemblage composition were apparent between the boreal forest sites in the south and the arctic tundra sites in the north (Pienitz et al. 1995; Gregory-Eaves et al. 1999). Here, to explore the similarities or dissimilarities in the diatom assemblages between the two training sets, a detrended correspondence analysis grouping all (259) species was carried out. The detrended correspondence analysis shows a clear distinction between species assemblages from the 58 lakes in the Yukon data set and the 51 lakes in the Alaskan data set (Fig. 2). The percentage of cumulative variance captured by the first two axes is 11.4% of the species data. The first two axes of the detrended correspondence analysis are significant according to Monte Carlo permutation tests (with 199 unrestricted permutations, $p \leq 0.05$).

A detrended canonical correspondence analysis was carried out (Fig. 3) to test if the dissimilarity between the diatom assemblages can be explained by environmental differences between the two regions. Only if the variables that

Fig. 2. Detrended correspondence analysis (DCA) plot showing diatom assemblage dissimilarities between Alaskan and Yukon lakes. Solid circles represent lakes from the Yukon and Northwest Territories, and open circles represent Alaskan lakes.

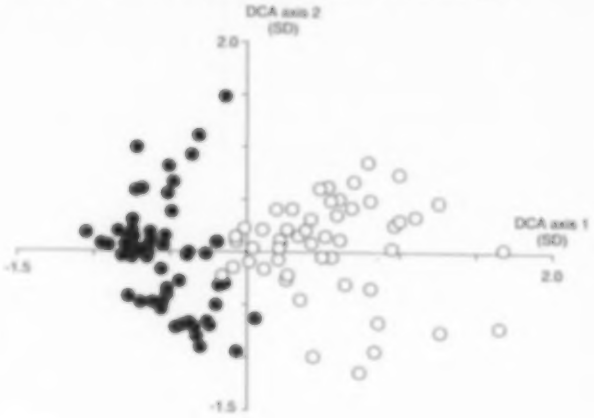
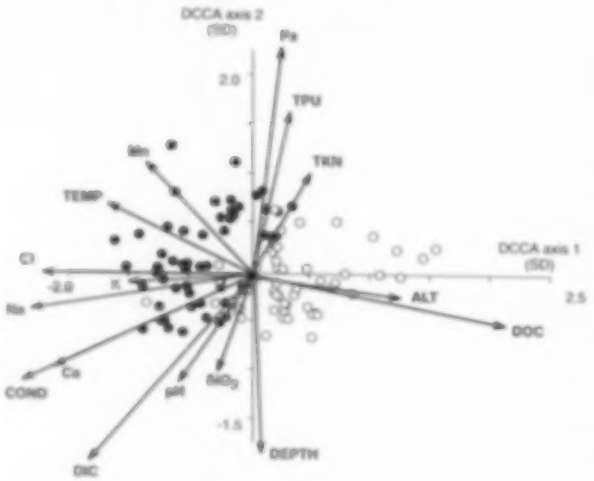


Fig. 3. Detrended canonical correspondence analysis (DCCA) plot of the 109-lake data set. Solid circles represent lakes from the Yukon and Northwest Territories, and open circles represent Alaskan lakes. TEMP, water temperature; DEPTH, water depth; TPU, total phosphorus unfiltered; TKN: total Kjeldahl nitrogen; COND, conductivity; DOC, dissolved organic carbon; DIC, dissolved inorganic carbon.



cover different ranges in the two regions explain a great proportion of species variation we can ensure that assemblage dissimilarity is due to these environmental variables. The percentage of cumulative variance in the species–environment relationship captured by the first two detrended canonical correspondence analysis axes is 35.45%, with eigenvalues of 0.284 for axis 1 and 0.157 for axis 2. All canonical axes are significant according to Monte Carlo permutation tests (with 199 unrestricted permutations, $p = 0.018$). In the detrended canonical correspondence analysis plot, ordination of the lakes on the first axis shows a separa-

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tion between Yukon and Alaskan lakes. From the relative position of the lakes in the environmental space, it is clear that species assemblages in Alaska are generally associated with more DOC-rich and more high-altitude conditions than species assemblages in the Yukon and Northwest Territories.

Initial training set based transfer functions

From the initial training set of 259 species and 109 sites, diatom – artificial neural networks based models for water temperature, water depth, and DOC were built. We present plots of observed values versus predicted values (Figs. 4*a*–4*c*). The predictive power of each model is low as expressed here as the relative measure of relationship strength (r^2 jackknife) between the predicted and observed values. The absolute measures of uncertainty associated with the predictions (i.e., the RMSE of prediction (RMSEP)) of each model are approximately twice those generally obtained in other studies of diatom-based water temperature, water depth, and DOC models (e.g., Pienitz et al. 1995; Fallu and Pienitz 1999; Gregory-Eaves et al. 1999). Moreover, the relationships between observed and predicted values are not linear for either the water temperature model or the DOC model, suggesting that these models are strongly biased.

Constrained training set based transfer functions

More optimal training sets were obtained by pruning the initial full species data set (259) according to the contribution of the diatom species to the performance of either the water temperature, water depth, or DOC model. By using the skeletonization algorithm until the "apparent" performances (RMSE) of the models increased over 10% from the minimum, the species-tailoring procedure reduced the initial data set by 65.4% (260 to 90 species) for the water temperature based model, 59.6% (259 to 105) for the water depth based model, and 49.2% (259 to 132) for the DOC-based model. Species composition of the three subtraining sets is shown in Appendix A. Only 24 species (9.2% of the initial full training set) are common to all three tailored sets. Forty-seven species (18.1%) are common to the water temperature and water depth training sets, 50 species (19.2%) to the water temperature and DOC sets, and 55 species (21.1%) to the water depth and DOC models. That the pruning algorithm selects different groups of species indicates that the relative importance of several species to the apparent statistics of a model is critically dependent on the environmental variable considered. Nevertheless, the question remains as to what extent each group of species can be used to improve the predictions of the environmental variable for which they were selected. In other words, how does the exclusion of species improve the cross-validated predictive performances of the models? To answer this question, we built cross-validated (leave-one-out jackknifing) models for each of the three environmental variables using their corresponding subtraining set (plots of observed versus predicted values are presented in Figs. 4*d*–4*f*). The predictive power of each pruned training set based model is improved when compared with the corresponding initial training set based models (Figs. 4*d*–4*f*). The strength (r^2 jackknife) of the relationship between the predicted and observed values increased from 0.34 to 0.68 for water temperature, from 0.60 to 0.77 for water depth, and from 0.33 to 0.67 for DOC. This leads to a decrease in the absolute measure of uncertainty associated with the predictions of each model. The improvement in predictive power of each constrained model is statistically significant ($F = 1.92$, 1.7, and 1.79; $p = 0.0074$) for temperature, depth, and DOC, respectively.

Discussion

Species selection and model improvement

The proposed environmentally dependent pruning method used here allowed us to build tailored training sets for diatom-based water temperature, water depth, and DOC models. The constrained training sets were built separately from the initial training set according to the relative contribution of each species to each of the three variables studied. By removing noncontributing species, the predictive power of the models increased significantly in all three cases, suggesting that pruning is an efficient method for improving model performance. Indirectly, these results also imply that the species that were removed by the pruning method were in fact corrupting the models based on all species. Moreover, the species removal also improved the prediction characteristics of the models. For example, when all species were included in the water temperature model, the predictions never exceeded 20 °C, while the predictions were very close to the observations (up to 24 °C) when only the species that seemed to be useful to model water temperature were included. Clearly, the removal of noncontributing species is beneficial, both to improve prediction power and to reduce model bias.

Our results clearly demonstrate that the assumption that all species are ecologically relevant and therefore contribute to the accuracy of the prediction is questionable. Nevertheless, the question of how the noncontributing species affect the model remains difficult: are noncontributing species simply a source of random noise or is there a more complex coupling between the species and their environment? By analogy with simple modeling techniques such as multiple regression, the inclusion of species that carry no information about their environment should not negatively affect performance of a model: the modeling procedure should normally simply ignore them by assigning them very little weight. However, because species removal actually improved model performance, our results suggest that these species had a genuinely corrupting influence. In our view, this is most likely conceivable for species that are multiply determined (i.e., for species that are strongly influenced by more than one environmental gradient). Unless these influencing gradients are always correlated to the same extent and in the same way, no modeling technique can reasonably cope with possibly conflicting environmental signals.

While these multiply determined species are probably an important source of model corruption, there may also be other ways by which variations in the abundance of certain species actually confound a model. For example, there may be several alternative stable species assemblages for a given lake driven by interspecific relationships among the diatoms. As such, these types of relationships are never considered in model building, although they are likely to occur in nature. However, we know of no method that is able to assess the relative importance of these confounding influences. To this extent, the question of how noncontributing species affect

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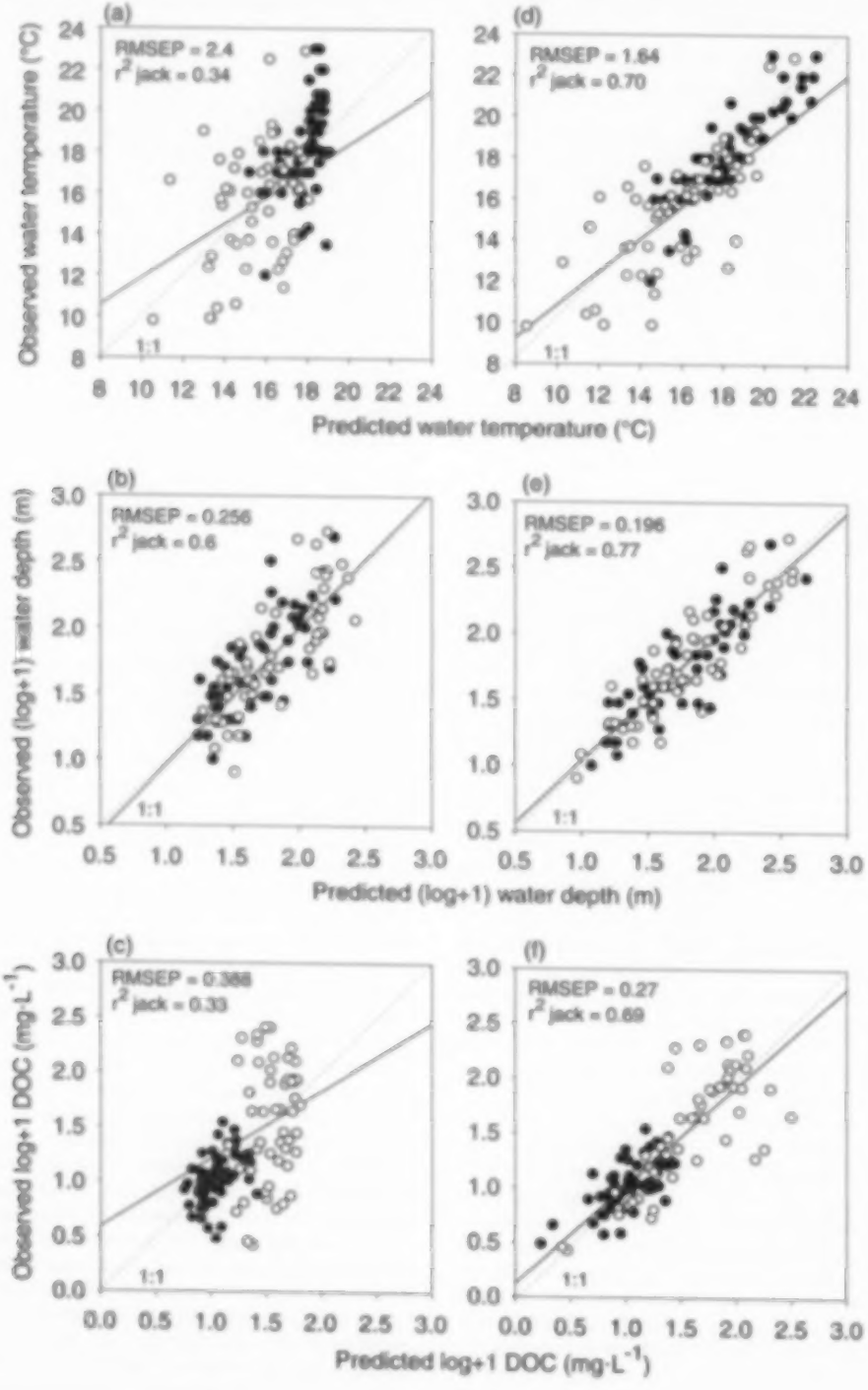
Fig. 4. Plots of observed against jackknife-predicted values for the water temperature model, water depth model, and DOC model (*a–c*) when all species are used and (*d–f*) when pruned training sets are used. The jackknife-predicted values are based on a validation set (leave-one-out). Fitted lines are based on model I regression. Solid circles represent lakes from the Yukon and Northwest Territories, and open circles represent Alaskan lakes.



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the predictive capacities of a model remains open. Until such a question can be addressed, we argue that the best palaeolimnological models will be those tailored only with the appropriate species (i.e., those that are useful in a predictive sense). In this context, pruned models for water temperature, water depth, and DOC do not necessarily contain species that are exclusively influenced by only one of these variables. Indeed, a species that is multiply determined can still be useful if at least some of the information that it carries can, in some sense, be generalized. This appears to be the case for all species that are common to all tailored training sets (9.2% of the species in our case). Conversely, the species that are multiply influenced but for which no generalization can be achieved will necessarily be eliminated by the pruning algorithm.

Toward independent transfer functions

That noncontributing species can corrupt the empirical predictive power of the models suggests that any changes in the distribution and abundance of these species in the past could affect their reconstruction capabilities. This is an important lacunae of unpruned models. Because the distribution and abundance of these noncontributing and possibly corrupting species may be strongly influenced by several variables (physical, chemical, and (or) biological) characteristic of the lake system, changes in any of these environmental parameters will alter their abundance. Thus, we could wrongfully infer changes in the variable of interest even if it remained unchanged. Because of this, we suggest that the removal of noncontributing taxa can potentially reduce the effects of other environmental influences. We contend that tailored models are probably less sensitive than others and more independent because they are specifically designed to quantify the changes of one environmental variable using only species that respond to this variable in a way that can be generalized.

Until now, the effects of multiple influence and interaction of environmental gradients (correlated or not) on species assemblages were only partially addressed in the design phase of palaeolimnological studies by selecting lakes to be included in the training set (S. Hausmann and F. Kienast, Paleolimnology–Paleoecology Laboratory, Centre d'Études Nordiques, Département de Géographie, Université Laval, Québec, QC G1K 7P4, Canada, unpublished data). However, while a preselection is often possible in certain regions, mainly for those where information on lakes is easy to obtain before sampling, sampling is limited and logistically difficult and expensive, for example, in remote northern regions. In these regions, controlling the number of influencing variables by reducing the number of sites in an existing training set is one alternative way to constrain the multiple environmental influences on species. In this case, a subtraining set of selected sites is defined in which the environmental variable of interest has the largest range possible but in which the ranges of secondary variables are also kept narrow (S. Hausmann and F. Kienast, unpublished data). However, this a posteriori selection could be problematic for at least two reasons. First, the number of sites, often an important parameter in the success of the modeling approach, could end up being too small if many secondary variables are detected in the original training set. Second, and more importantly, a model based on such a "site-selected" training set where few situations of interaction and (or) multiple influences are structuring the species data would be incapable of implementing these situations. As a result, such models will perform poorly when applied to down-core species data if interactions and (or) multiple influences occurred in the past. This second problem is also relevant to models based on modern training sets where an a priori selection of sites is made to avoid the effects of secondary gradients.

Ideally, the implementation of every organism–environment relationship should be based on modern training sets where situations of multiple influences and (or) interactions structure species assemblages: only a model that has the possibility of "learning" from multivariate patterns will have the potential to give realistic inferences when applied to multiply induced past assemblage data. Thus, the more examples of similar situations of multiple influences or interactions occur in a training set, the more a model will be capable of implementing these situations. However, if a model is not able to learn from some situations because too few examples of these occur in a given training set, then these situations need to be avoided. Therefore, we suggest that more effort should be made toward the development of efficient calibration models in which only nongeneralized situations of multiple influences and interactions are avoided (i.e., like our pruning algorithm do) rather than toward the development of calibration models in which all situations of multiple influence or interaction (i.e., generalizable and not) are avoided (i.e., like in methods based on a priori or a posteriori selection of sites). In other words, more attention should be given to build efficient univariate-based models from a multivariate organism–environment relationships training set rather than attempting to build univariate models from a pseudo-univariate organism–environment relationships training set. To be efficient, an appropriate univariate model (based on multivariate relationships) should be capable of reaching the two following goals. First, the model should have the ability to implement only the generalizable relationships between assemblage data and each structuring environmental variable (i.e., where species that suffer from nongeneralizable multivariate interaction are excluded). Second, it should have the capacity to make independent predictions. The method proposed in this study is designed to reach these two goals: the selection of species is made to create an optimal model for a given variable by removing species whose distributions are independent of the variable of interest. In addition, by making an environmentally dependent selection of species to be included in a particular training set, a transfer function based on these species will be quasi-independent (a certain dependence will occur only in cases where species are common to several subtraining sets).

We believe that these observations to be important, as independent transfer functions are required in situations where any reconstructed environmental variable may be confounded by the influence of other factors. For example, few researchers have attempted to model water depth because changes in nutrient concentration and (or) light quality may or may not covary with lake level fluctuations (Wolin and Duthie 1999). Similarly, reconstruction of lake depth is problematic because changes in lake level could be the con-

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sequence of changes in temperature and (or) the result of changes in relative humidity. The application of our three quasi-independent diatom transfer functions for reconstruction of past changes in lake depth, lake water temperature, and DOC concentration could provide substantial insight into the magnitude of past climatic and environmental changes in northwestern Canada and Alaska.

In conclusion, in this study, we have applied a method that is designed to build tailored palaeolimnological models in situations were several important environmental variables structure species data in a training set. In contrast with the idea of a priori or a posteriori selection of lakes to reduce secondary gradients, the proposed method deals with the selection of a subset of numerically useful species. The reasoning behind the approach is that the implementation of a single gradient-based organism–environment relationship should use only species that are comprehensively influenced by the variable of interest. Such an approach based on taxon selection appears to be attractive for two reasons. First, the selection of species is made to create an optimal model for a given variable by removing taxa with distributions that are independent of the variable of interest. The resulting tailored training set can then be used to develop more powerful models. Second, several quasi-independent models of species–environment relationships could be developed from the same original training set because each model will be based on different subsets of relevant species. Once validated using other data sets, this method could prove a very useful tool for developing several tailored transfer functions from the same modern training set and (or) from training sets where several environmental variables are important in structuring species assemblage data.

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Appendix A

Table A1. Selected diatom species for the water temperature (TEMP), water depth (DEPTH), and dissolved organic carbon (DOC) models.

Species	Occurrence	TEMP	DEPTH	DOC
Fragilaria pinnata	99	Selected	Selected	Selected
Achnanthes minutissima (tribe)	105	Selected	Selected	Selected
Fragilaria brevistriata	81		Selected	Selected
Cyclotella stelligera	73	Selected		Selected
Fragilaria construens var. *venter*	62	Selected	Selected	Selected
Fragilaria pinnata (coarse form)	51	Selected	Selected	
Navicula minima	70			
Navicula cryptotenella	71	Selected	Selected	Selected
Navicula seminulum	61	Selected	Selected	
Nitzschia fonticola	62	Selected	Selected	Selected
Fragilaria brevistriata var. *papillosalinflata*	66	Selected		Selected
Navicula pupula	72			Selected
Amphora pediculus	52			Selected
Achnanthes pusilla	55	Selected		Selected
Cymbella microcephala	52	Selected	Selected	Selected
Cyclotella pseudostelligera	34	Selected		
Fragilaria construens	39		Selected	Selected
Brachysira vitrea/*Anomoeoneis vitrea*	53	Selected		Selected
Fragilaria pinnata var. *intercedens*	41			Selected
Asterionella formosa	33	Selected	Selected	Selected
Fragilaria construens var. *pumila*	28	Selected		Selected
Navicula vitiosa	42	Selected	Selected	Selected
Fragilaria capucina var. *gracilis*	36	Selected	Selected	Selected
Achnanthes subatomoides	48	Selected		
Cyclotella rossii	25		Selected	Selected

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Table A1 (*continued*).

Species	Occurrence	TEMP	DEPTH	DOC
Fragilaria pseudoconstruens	32	Selected	Selected	Selected
Cyclotella tripartita	20	Selected	Selected	Selected
Achnanthes conspicua	29			
Cymbella silesiaca	53	Selected	Selected	
Fragilaria tenera	26	Selected	Selected	
Navicula capitata var. *hungarica*	33		Selected	Selected
Fragilaria nanana	22	Selected		Selected
Achnanthes euchlandii	33		Selected	
Amphora libyca	43			Selected
Gomphonema parvulum	39	Selected		Selected
Navicula disjuncta	32			Selected
Cyclotella michiganiana	20	Selected	Selected	Selected
Cyclotella cf. *ocellata*	18	Selected		
Fragilaria famelica	21	Selected		
Navicula cryptocephala	28	Selected		
Cymbella cf. *angustata*	19			Selected
Cymbella gracilis	27	Selected	Selected	Selected
Nitzschia perminuta	28		Selected	
Aulacoseira subarctica	13	Selected	Selected	
Cocconeis placentula var. *euglypta*	24			
Achnanthes lanceolata aff. sp. *lanceolata*	25		Selected	Selected
Navicula cryptotenella fo. PISCES	16	Selected	Selected	
Navicula radiosa	38	Selected		Selected
Calonеis bacillum	24	Selected	Selected	
Pinnularia interrupta/*P. biceps*	37	Selected		
Fragilaria virescens var. *exigua*	15		Selected	
Cocconeis placentula	12			
Navicula meniculus	19	Selected	Selected	Selected
Cyclotella delicatissima	9	Selected	Selected	Selected
Diploneis oculata	34		Selected	
Stauroneis anceps	30			Selected
Stauroneis anceps var. *gracilis*	17	Selected		
Aulacoseira alpigena	10		Selected	Selected
Cyclotella bodanica	15	Selected	Selected	
Cyclotella bodanica var. *lemanica*	12	Selected	Selected	Selected
Achnanthes lanceolata ssp. *frequentissima*	14			Selected
Navicula laevissima	34			Selected
Navicula submuralis	16			Selected
Amphora inariensis	22	Selected	Selected	
Nitzschia amphibia	16		Selected	Selected
Nitzschia palea	24	Selected	Selected	Selected
Synedra radians	12	Selected		
Stauroneis phoenicenteron	20			
Navicula absoluta	15		Selected	
Navicula digitulus	17			Selected
Navicula schmassmannii	12		Selected	Selected
Nitzschia acicularis	20			
Aulacoseira distans var. *humilis*	11		Selected	Selected
Aulacoseira distans var. *nivalis*	6			Selected
Cyclotella comensis	12			Selected
Stephanodiscus alpinus	8	Selected	Selected	
Tabellaria flocculosa (strain IV)	25			
Diatoma tenue var. *elongatum*	26	Selected		
Fragilaria capucina	10	Selected	Selected	Selected
Fragilaria lapponica	7		Selected	
Eunotia incisa	13	Selected		Selected
Achnanthes altaica	9			

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Table A1 (*continued*).

Species	Occurrence	TEMP	DEPTH	DOC
Achnanthes curtissima	15		Selected	
Achnanthes impexiformis/impexa	14			Selected
Achnanthes laterostrata	18	Selected		
Achnanthes marginulata	14	Selected	Selected	Selected
Gyrosigma spenceri	10			
Amphipleura kriegeriana	16			Selected
Navicula disjuncta fo. short (<15 μm)	9			Selected
Navicula elginensis	10		Selected	Selected
Navicula indifferens	7			Selected
Navicula mediocris	11			
Navicula rhynchocephala	18			Selected
Gomphonema gracile	12			
Nitzschia graciliformis	16	Selected		Selected
Nitzschia gracilis	20	Selected	Selected	
Cyclotella atomus	6		Selected	
Cyclotella comensis fo. AK 1	10		Selected	
Stephanodiscus cf. *medius*	10			Selected
Stephanodiscus hantzschii	6		Selected	Selected
Fragilaria capucina var. *rumpens*	8			
Fragilaria crotonensis	5		Selected	
Fragilaria pinnata var. *lancettula*	8		Selected	Selected
Fragilaria robustal F. pseudoconstruens var. *bigibba*	13	Selected		
Fragilaria vaucheriae	37	Selected	Selected	Selected
Eunotia intermedial E. vanheurckii	8	Selected		
Achnanthes chlidanos	15			
Achnanthes gracillima	6	Selected	Selected	Selected
Achnanthes levanderi	17	Selected		Selected
Diploneis oblongella	13			
Neidium ampliatum	19			Selected
Navicula minuscula	16		Selected	
Navicula oblonga	5			
Navicula pseudoscutiformis	37			
Cymbella hebridica	10	Selected	Selected	
Cymbella incerta	13			Selected
Cymbella perpusilla	8			Selected
Amphora thumensis	8			Selected
Gomphonema minutum	4	Selected	Selected	
Nitzschia amphibioides	10		Selected	Selected
Rhoicosphenia abbreviata	7		Selected	Selected
Aulacoseira ambigua	9			
Cyclotella rossii fo. AK 1 (tripartita)	8			
Stephanodiscus parvus	4		Selected	Selected
Tabellaria flocculosa (strain III)	10		Selected	Selected
Fragilaria construens var. *binodis*	10			
Eunotia bilunaris	17			
Achnanthes clevei	10			
Achnanthes microcephala	9	Selected		Selected
Achnanthes rosenstockii	5		Selected	
Achnanthes scotica	11	Selected		Selected
Achnanthes ventralis	17	Selected	Selected	
Frustulia rhomboides var. *crassinervia*	7		Selected	
Diploneis marginestriata	8			Selected
Stauroneis smithii var. *minima*	4			Selected
Brachysira brebissonii/Anomoeoneis brachysira	9	Selected	Selected	
Navicula absoluta fo. 1	12			Selected
Navicula bryophila	15			
Navicula cocconeiformis	23			

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Table A1 (*continued*).

Species	Occurrence	TEMP	DEPTH	DOC
Navicula halophila	8			Selected
Navicula juernefeltii	18		Selected	Selected
Navicula modica	10	Selected		Selected
Navicula cf. *oppugnata*	3			Selected
Navicula vitabunda	20			Selected
Calonеis silicula	19	Selected		Selected
Pinnularia microstauron	19	Selected	Selected	
Cymbella naviculiformis	12			
Amphora fogediana	15		Selected	
Nitzschia dissipata	8			
Nitzschia radicula	7			Selected
Nitzschia recta	18	Selected		Selected
Epithemia adnata	6		Selected	
cf. *Achnanthes ricula*	8			
Aulaconeira italica	3			Selected
Aulacoseira valida	5			
Stephanodiscus minutulus	3		Selected	Selected
Tabellaria flocculosa (strain I)	19	Selected	Selected	Selected
Fragilaria cyclopum/Hannaea arcus	12			
Fragilaria ulna/S. ulna	11		Selected	Selected
Fragilaria delicatissima	7			Selected
Eunotia praerupta	13			
Eunotia faba	6			
Eunotia rhynchocephala	6	Selected		Selected
Achnanthes carissima	8			
Achnanthes exigua var. *heterovalva*	4			Selected
Achnanthes flexella var. *alpestris*	11			Selected
Achnanthes oestrupii	11			
Achnanthes saccula	9			
Diploneis elliptica	11		Selected	
Stauroneis kriegerii	5	Selected		
Navicula arvensis	6		Selected	Selected
Navicula jaagii	4	Selected		Selected
Navicula lenzii	5		Selected	
Navicula leptostriata	7		Selected	
Navicula pseudanglica	4	Selected		
Navicula pseudoventralis	7	Selected		
Navicula seminuloides	4			
Navicula subhamulata	4			
Navicula subrotundata	11		Selected	Selected
Navicula trivialis	8		Selected	Selected
Calonеis tenuis	3			Selected
Cymbella amphicephala	14	Selected		Selected
Cymbella cf. *cesatii*	7			
Gomphonema angustatum	7		Selected	Selected
Gomphonema pumilum	6			Selected
Nitzschia liebtruthii	5		Selected	
Nitzschia pura	17			
Nitzschia valdestriata	8			Selected
Simonsenia delognei	5		Selected	Selected
Denticula tenuis	3			
Stenopterobia curvula	3			Selected
cf. *Nitzschia bacillum*	5		Selected	
Tabellaria fenestrata	7	Selected	Selected	
Diatoma mesodon	4			
Fragilaria capucina var. *mesolepta*	7		Selected	Selected
Fragilaria leptostauron	6	Selected	Selected	Selected

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Table A1 (*continued*).

Species	Occurrence	TEMP	DEPTH	DOC
Fragilaria parasitica	27	Selected	Selected	
Fragilaria neoproducta	4	Selected		Selected
Eunotia flexuosa	5			Selected
Eunotia monodon	4			Selected
Eunotia paludosa	3			
Eunotia circumborealis	4			
Cocconeis cf. diminuta	3		Selected	Selected
Cocconeis neothumensis	7			
Cocconeis placentula var. *lineata*	6			
Achnanthes helvetica	3		Selected	Selected
Achnanthes didyma	14		Selected	Selected
Achnanthes flexella	6		Selected	Selected
Achnanthes lacus-vulcani	8			Selected
Achnanthes linearis	13			
Achnanthes petersenii	16		Selected	Selected
Achnanthes peragalli	6		Selected	
Achnanthes ziegleri	4			Selected
Gyrosigma acuminatum	3			Selected
Amphipleura pellucida	8		Selected	Selected
Frustulia rhomboides	3			Selected
Frustulia rhomboides var. *saxonica*	6		Selected	
Diploneis parma/subovalis	11			
Stauroneis producta	3			
Stauroneis smithii	12			
Brachysira zellensis/Anomoeoneis brachysira var. *zellensis*	5			
Brachysira minor	5	Selected	Selected	
Navicula bacillum	3			
Navicula difficillimalarvensis	3		Selected	
Navicula explanata	13	Selected	Selected	
Navicula gerloffii	5			
Navicula ignota var. *palustris*	5	Selected	Selected	Selected
Navicula laevissima var. *perhibita*	3	Selected		Selected
Navicula libonensis	3		Selected	
Navicula mediocomvexa	6	Selected		Selected
Navicula menisculus fo. AK 1	3			Selected
Navicula pseudolanceolata	5			
Navicula similis	5			
Navicula soehrensis var. *hassiaca*	9			
Navicula soehrensis	6	Selected	Selected	
Navicula subtilissima	4	Selected		Selected
Navicula salinarum	4			
Navicula tuscula	4			
Navicula veneta	5	Selected		
Pinnularia balfouriana	10			
Pinnularia maior	7			
Pinnularia nodosa	8			Selected
Pinnularia viridis	9		Selected	
Cymbella cistula	9			Selected
Cymbella cymbiformis	6			Selected
Cymbella falaisensis	5	Selected	Selected	
Cymbella hustedtii	3			Selected
Cymbella incerta var. *crassipunctata*	5			Selected
Cymbella lapponica fo. short	6			Selected
Cymbella minuta	13	Selected		
Gomphonema acuminatum	8	Selected		Selected
Gomphonema lateripunctatum	3	Selected		Selected
Gomphonema olivaceum	4			

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Table A1 (*concluded*).

Species	Occurrence	TEMP	DEPTH	DOC
Nitzschia alpina	9	Selected		Selected
Nitzschia rectiformis	8			
Nitzschia solita	3	Selected	Selected	
Nitzschia supralitorea	3			
Epithemia sorex	5		Selected	
cf. *Navicula trivialis*	4		Selected	

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Long-term trends in age-specific recruitment of sockeye salmon (*Oncorhynchus nerka*) in a changing environment

Carrie A. Holt and Randall M. Peterman

Abstract: Sibling – age-class (sibling) models, which relate abundance of one age-class of adult sockeye salmon (*Oncorhynchus nerka*) to abundance of the previous age-class in the previous year, are commonly used to forecast abundance 1 year ahead. Standard sibling models assume constant parameters over time. However, many sockeye salmon populations have shown temporal changes in age-at-maturity. We therefore developed a new Kalman filter sibling model that allowed for time-varying parameters. We found considerable evidence for long-term trends in parameters of sibling models for 24 sockeye salmon stocks in British Columbia and Alaska; most trends reflected increasing age-at-maturity. In a retrospective analysis, the Kalman filter forecasting models reduced mean-squared forecasting errors compared with standard sibling models in 29%–39% of the stocks depending on the age-class. The Kalman filter models also had mean percent biases closer to zero than the standard models for 54%–94% of the stocks. Parameters of these sibling models are positively correlated among stocks from different regions, suggesting that large-scale factors (e.g., competition among stocks for limited marine prey) may be important drivers of long-term changes in age-at-maturity schedules in sockeye salmon.

Résumé : Les modèles de fraterie–classes d'âge (« sibling models »), qui mettent en relation l'abondance d'une classe d'âge d'adultes de saumons rouges (*Oncorhynchus nerka*) à l'abondance de la classe d'âge précédente de l'année antérieure, servent souvent à prédire l'abondance 1 année d'avance. Les modèles de fraterie courants assument que les paramètres sont constants dans le temps. Cependant, plusieurs populations de saumons rouges subissent des changements temporels de l'âge à la maturité. Nous avons donc mis au point un nouveau modèle de fraterie avec un filtre de Kalman qui tient compte de paramètres variables dans le temps. Il y a de nombreux indices qu'il existe des tendances à long terme dans les paramètres des modèles de fraterie chez 24 populations de saumons rouges de la Colombie Britannique et de l'Alaska; la plupart des tendances indiquent un âge plus avancé à la maturité. Dans une analyse rétrospective, les modèles prédictifs à filtre de Kalman réduisent le carré des erreurs moyennes de prédiction par comparaison aux modèles standard de fraterie chez 29–39 % des stocks, selon la classe d'âge. Les modèles avec filtre de Kalman ont aussi des pourcentages d'erreurs moyennes plus proches de zéro que les modèles standard chez 54–94 % des stocks. Les paramètres de ces modèles de fraterie sont en corrélation positive d'un stock à l'autre dans les différentes régions, ce qui laisse croire à l'existence de facteurs agissant à grande échelle (e.g., la compétition entre les stocks pour un nombre limité de proies marines) qui peuvent être des causes majeures des changements de l'âge à la maturité observés chez le saumon rouge.

[Traduit par la Rédaction]

Introduction

Forecasting models are used widely in management of Pacific salmon (*Oncorhynchus* spp.) fisheries; good forecasts improve economic gains while reducing the chance of conservation problems. Inaccuracies in forecasts can result in either short-term economic costs from reduced harvest if too few fish are forecasted compared with actual returns or conservation risks if forecasts are much higher than actual returns and result in harvests that are too high. To improve forecasting accuracy, we revised one type of forecasting model, the sibling – age-class relation (henceforth called the sibling model) and compared the performance of this new version with the standard sibling model.

Sibling models take advantage of the life history of Pacific salmon by forecasting the abundance of one age group based on its siblings' abundance, i.e., abundance of the previous age-class that was estimated in the previous year. In sockeye salmon (*Oncorhynchus nerka*), for example, siblings, or offspring from a given brood class that were spawned in a given year, mature at various ages (from age 3 years to as old as age 7 in some stocks). For instance, a

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C.A. Holt[1] and R.M. Peterman. School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.

[1]Corresponding author (e-mail: cholt@sfu.ca).

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sibling model can forecast the abundance of 5-year-old sockeye recruits from the abundance of its 4-year-old siblings that were estimated in the previous year as they returned to coastal waters.

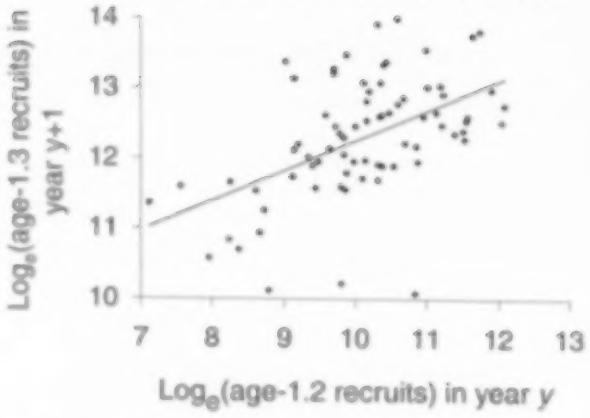
Such sibling models are attractive because fish in the age group represented by the independent variable share similar environmental conditions with fish in the forecasted age group. Specifically, siblings that smolt in the same year (i.e., after either one or two winters in fresh water) but that mature and return to fresh water *at different ages* experience similar conditions during early ocean residence, which is the most critical period for marine mortality (Groot and Margolis 1991). Therefore, siblings that return to fresh water in successive years typically have similar relative variation in recruitment over time. For example, abundance of age-4 recruits to Chignik Lake, Alaska, that spend one winter in fresh water and two winters in the ocean (denoted age 1.2) correlates well with abundance of sibling age-5 recruits from the same brood year that also spend one winter in fresh water but three winters in the ocean (denoted age 1.3) (Fig. 1).

Sibling models are used widely for forecasting sockeye salmon recruitment in British Columbia (Rutherford and Wood 2000) and Alaska (Cross and Gray 1999; Hilborn et al. 1999). These models have the advantage of generating preseason forecasts by using more recent stock information (age-specific returns from the previous year) than stock–recruitment forecasting models, which use spawner abundances 3–7 years prior to recruitment. Therefore, sibling forecasting models may better reflect recent changes in recruitment patterns than traditional stock–recruitment forecasting models or their variants that incorporate environmental covariates. Nevertheless, there is still considerable variation in recruitment that is not explained by sibling models (e.g., Fig. 1).

These forecasts of recruitment may be imperfect in part because the main assumption of the sibling model may not be valid. In particular, the slope and intercept parameters of the model may vary over time owing to long-term changes in the proportion of fish that mature at different ages. For example, mean age-at-maturity (affecting proportions of recruits of each age) has shown a common increasing trend among 31 sockeye salmon stocks in British Columbia and Alaska from the 1960s to the 1990s (Pyper et al. 1999).

There are at least two reasons why temporal trends in parameters of sibling models have not been analyzed in depth before. First, fisheries scientists have typically attributed changes in the age-specific recruitment to random sources of variability and thus have assumed constant parameters over time for their forecasting models. In some cases, year-to-year changes in age-specific recruitment have been attributed to changes in body size of recruits. For example, in years where the body size of recruits of younger siblings is small, a greater than normal proportion of older siblings is expected to return the following year (L. Fair, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518-1599, USA, personal communication). However, long-term trends have not been investigated for sibling models, even though they have been identified in parameters of other models of salmon population dynamics (e.g., productivity parameter of stock–recruitment models for sockeye salmon; Peterman et al. 2003). Second, only recently has there been an assessment of the reliability of various methods for estimating temporal trends, or even changes to new persistent levels, in parameters of salmon models. Using Monte Carlo simulations, Peterman et al. (2000) found that if stock productivity changes over time, a model that allows for variation in the a parameter of the Ricker stock–recruitment model and that is estimated using a Kalman filter tracks these changes better than a model with constant parameters, even if the latter model is updated annually. Such models with time-varying parameters also performed better in terms of mean-squared error than standard models (Peterman et al. 2000). Although that analysis pertained to the time-varying productivity parameter in stock–recruitment relations, its results suggest that a similar Kalman filter approach could be used to determine whether long-term changes are occurring in parameters of sibling models.

Fig. 1. Sibling – age-class relation between the logarithm of the abundance of age-1.2 adult sockeye salmon recruits (fish spending one winter in fresh water and two winters in the ocean) in year y and age-1.3 recruits (fish spending one winter in fresh water and three winters in the ocean) in year $y + 1$, for Chignik Lake, Alaska Peninsula, for 1918–1994 ($r = 0.52$, $P < 0.001$).



Our overall goal was to improve forecasts of sockeye salmon recruitment using a revised sibling model with time-varying parameters. We had three specific research objectives. (*i*) We used a Kalman filter estimation scheme in conjunction with a sibling model that assumed time-varying parameters to identify whether there are long-term trends or persistent changes in parameters of sibling models for British Columbian and Alaskan sockeye salmon stocks, as opposed to just year-to-year variation. (*ii*) We used historical data in a retrospective analysis to compare the reliability of forecasts from the model that allows for temporal changes in its parameters with forecasts from the standard sibling model that assumes constant parameters over time. (*iii*) We also examined potential physical and biological drivers of changes in parameters of sibling models.

Methods

Biological data

We analyzed 41 previously compiled time series of age-specific recruitment data (catch and numbers of spawners, or

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Table 1. Summary of 24 sockeye salmon stocks analyzed with sibling models.

Region	Stock	Brood year	N	Age-class stanza	Lag 1	Average recruitment in 1000s (x.2, x.3)	Source[a]
Bristol Bay	Wood	1952–1996	45	1.2 vs. 1.3	0.31*	1297, 1161	Michael Link
			45	2.2 vs. 2.3	–0.04	179, 80	
	Ugashik	1952–1996	45	1.2 vs. 1.3	–0.09	604, 661	
			45	2.2 vs. 2.3	0.05	823, 447	
	Togiak	1952–1996	45	1.2 vs. 1.3	0.39*	116, 314	
			45	2.2 vs. 2.3	0.07	31, 35	
	Naknek	1952–1996	45	1.2 vs. 1.3	0.25*	503, 1403	
			45	2.2 vs. 2.3	0.14	711, 789	
	Kvichak	1952–1996	45	1.2 vs. 1.3	–0.05	2935, 1147	
			45	2.2 vs. 2.3	0.11	6742, 812	
	Igushik	1952–1996	45	1.2 vs. 1.3	0.13	195, 635	
			45	2.2 vs. 2.3	0.10	64, 54	
	Egegik	1952–1996	45	1.2 vs. 1.3	–0.07	503, 964	
			45	2.2 vs. 2.3	0.17	2659, 1732	
	Branch	1952–1996	45	1.2 vs. 1.3	–0.11	238, 167	
			45	2.2 vs. 2.3	–0.11	84, 33	
	Nuyakuk	1952–1983	32	1.2 vs. 1.3	0.35*	112, 638	
	Nushagak	1978–1994	17	1.2 vs. 1.3	–0.19	136, 751	
Alaska Peninsula	Nelson River	1981–1994	14	1.2 vs. 1.3	–0.30	53, 81	Patricia Nelson
			14	2.2 vs. 2.3	0.20	493, 185	
	Bear River	1981–1994	14	1.2 vs. 1.3	0.28	25, 39	
			14	2.2 vs. 2.3	0.32	400, 132	
Chignik	Black Lake	1918–1994	77	1.2 vs. 1.3	–0.07	58, 595	Patricia Nelson
			77	2.2 vs. 2.3	0.08	43, 208	
	Chignik Lake	1918–1994	77	1.2 vs. 1.3	0.12	39, 303	
			77	2.2 vs. 2.3	0.03	112, 475	
Kodiak	Frazer Lake	1966–1994	29	1.2 vs. 1.3	0.14	65, 35	Patricia Nelson
			30	2.2 vs. 2.3	0.26	181, 89	
	Late Upper Station	1970–1994	25	1.2 vs. 1.3	–0.02	86, 43	
			24	2.2 vs. 2.3	–0.18	207, 15	
	Early Upper Station	1969–1994	26	1.2 vs. 1.3	0.40*	17, 16	
			25	2.2 vs. 2.3	–0.25	50, 16	
	Ayakulik	1966–1994	29	1.2 vs. 1.3	–0.16	125, 120	
			30	2.2 vs. 2.3	–0.27	203, 112	
Cook Inlet	Upper Cook Inlet	1964–1993	30	1.2 vs. 1.3	–0.05	665, 2448	Ken Tarbox
			30	2.2 vs. 2.3	0.19	364, 676	
Prince William Sound	Copper River	1961–1994	34	1.2 vs. 1.3	–0.01	211, 966	Mark Willette
Northern British Columbia	Skeena River	1950–1994	45	1.2 vs. 1.3	0.10	890, 1015	Chris Wood
	Nass River	1967–1992	26	1.2 vs. 1.3	0.12	211, 150	Les Jantz
			25	2.2 vs. 2.3	0.36*	248, 41	
Central British Columbia	Long Lake	1973–1994	20	1.2 vs. 1.3	–0.29*	107, 200	Chris Wood
Fraser River	Pitt	1948–1994	47	1.2 vs. 1.3	–0.30*	25, 45	Jim Woodey and Mike Lapointe

Note: Region and stock describe a stock's location; N is the duration of the time series (years); age-class stanza shows which age-classes were the X and Y variables, respectively; lag 1 is the 1-year-lag autocorrelation coefficient in residuals of the standard sibling model that assumes constant parameters (an asterisk denotes a significant autocorrelation at the $\alpha = 0.05$ level); average recruitment is the average over each time series of each age-class in thousands of fish; and source describes from whom the data were obtained.

[a]All sources are personal communications. Mailing addresses are as follows:

Michael Link, LGL Alaska Research Associates, 1101 East 76th Avenue, Anchorage, AK 99518, USA.
Patricia Nelson, Alaska Department of Fish and Game, 1390 Buskin River Road, Kodiak, AK 99615, USA.
Ken Tarbox, Alaska Department of Fish and Game, 43961 Kalifornsky Beach Road, Suite B, Soldotna, AK 99669-8367, USA.
Mark Willette, Alaska Department of Fish and Game, 43961 Kalifornsky Beach Road, Suite B, Soldotna, AK, 99669-8367, USA.
Chris Wood, Conservation Biology Section, Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada.
Les Jantz, Fisheries and Oceans Canada, 417-2nd Avenue West, Prince Rupert, BC V8J 1G8, Canada.
Jim Woodey and Mike Lapointe, Pacific Salmon Commission, 600-1155 Robson Street, Vancouver, BC V6E 1B5, Canada.

escapement) from a total of 24 sockeye salmon stocks and stock complexes (i.e., aggregations of salmon populations that return to the same river) from eight different management regions in British Columbia and Alaska (Table 1; Fig. 2). Methods used by governmental agencies to estimate catches involved sampling at ports and performing stock identification and ageing of fish using scales, otoliths, and other means. These methods are reasonably reliable. Methods

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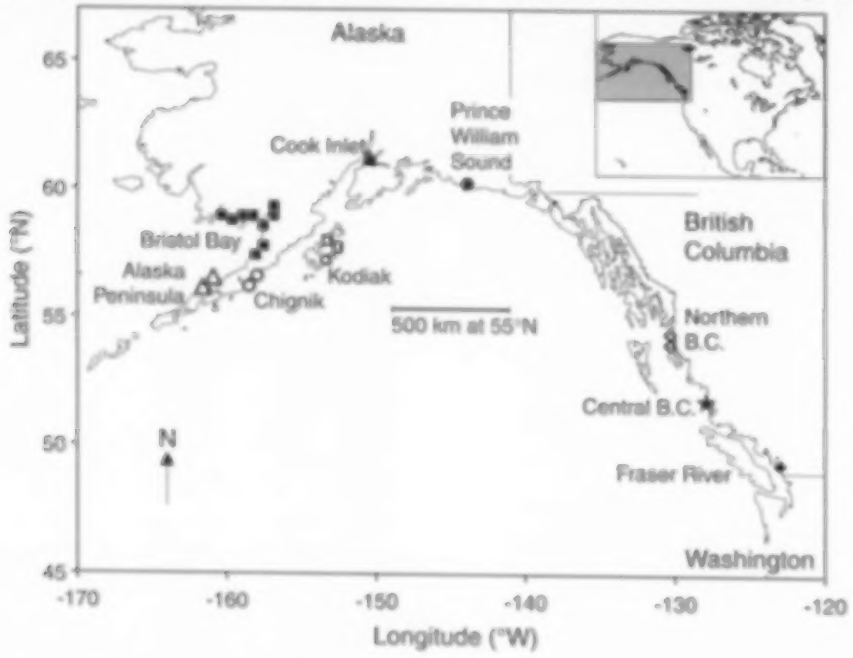
Fig. 2. Distribution of ocean-entry points for the 24 sockeye salmon stocks analyzed, which were categorized by region (inset shows location within North America). Regions are as follows: Fraser River, British Columbia (solid diamond), central British Columbia (star), northern British Columbia (open diamonds), Prince William Sound, Alaska (solid circle), Cook Inlet, Alaska (solid triangle), Kodiak, Alaska (open squares), Chignik, Alaska (open circles), Alaska Peninsula (open triangles), and Bristol Bay, Alaska (solid squares).



for estimating escapement are less reliable and varied somewhat among stocks. Those methods included counts at fences, foot surveys, mark–recapture studies, and aerial surveys. As elaborated later in the Discussion section, it is unlikely that errors in methods of estimating abundance caused the temporal trends observed here to be spurious. We analyzed recruitment data for both the relation between age-1.2 and age-1.3 recruits, or age-1.*z* stanza, and the relation between age-2.2 and age-2.3 recruits, or age-2.*z* stanza. We did not analyze other age stanzas because most stocks had too few data points for this type of analysis. To ensure sufficient sample sizes, we only included stocks with at least 10 consecutive years of age-specific recruitment data and substantial abundances for both *x*.2- and *x*.3 age-classes. The time series ranged in duration from 14 to 77 years.

Statistical analysis

Standard sibling model

The standard sibling model forecasts the abundance of recruits returning in year *y* in age-class *x.i* (spending *x* winters in freshwater, *i* winters in the ocean), $R_{x.i,y}$, from the abundance of recruits that returned the previous year, y – 1, in the previous age-class, *x.i*–1, $R_{x.i-1,y-1}$, (i.e., from the same brood year) (Peterman 1982)

$$(1) \qquad \log_e(R_{x.i,y}) = a + b\log_e(R_{x.i-1,y-1}) + v_t$$

Parameters *a* and *b* are specific to each age stanza, and v_t is a normally distributed random error term that reflects the multiplicative lognormal variation often found in marine survival rates of salmon (Peterman 1981), specific to each brood year, *t* (*t* = *y* – 4 for 4-year-old recruits and *t* = *y* – 5 for 5-year-old recruits). This standard sibling model, as well as its Kalman filter version described below, is merely a descriptive model of past data; it does not require a biological understanding of the mechanisms causing changes in recruitment.

A useful index of changing age structure, the *a* parameter of this sibling model, reflects the ratio of the abundance of recruits of age *x.i* in year *y* to the abundance of recruits of age *x.i*–1 in year *y* – 1, the latter raised to the power *b* (as is apparent when eq. 1 is rearranged)

$$(2) \qquad a = \log_e\left[\frac{R_{x.i,y}}{(R_{x.i-1,y-1})^b}\right] - v_t$$

The *a* parameter thus represents an index of age-at-maturity when comparing two age-classes. When the *b* parameter is equal to 1, the *a* parameter represents the logarithm of the ratio of recruitment from two successive age-classes in two successive return years (i.e., from the same brood year and ocean entry year). Higher values of *a* reflect a higher proportion of fish maturing at the older age for that particular age stanza than expected from the abundance of the next-younger-aged siblings. This *a* parameter is thus a more refined measure of shifts in adult recruitment across ages than the more commonly used mean age-at-maturity, which averages across several ages and obscures shifts between its composite pairs of ages. Mean age-at-maturity is also not very useful for forecasting abundance of recruits in a given year because those recruits are typically composed of two or

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more age-classes from two or more brood years; each of those brood years will likely have a somewhat different age structure.

Kalman filter model

We estimated temporal trends in the a parameter of sibling models using a Kalman filter model. The Kalman filter allowed us to estimate temporal trends in observed age-specific recruitment that were due to systematic process variation separately from random sources of variation that were independent of those trends (Chatfield 1996; de Valpine and Hastings 2002). The Kalman filter approach thus permitted annual estimation of effects of underlying processes influencing age-specific recruitment while reducing the confounding from random sources of variability independent of the trend. This Kalman filter technique has been used previously to estimate changes in productivity of sockeye salmon in British Columbia and Alaska as described by parameters of stock–recruitment models (Peterman et al. 2003).

This Kalman filter alternative to the standard sibling model consisted of two components. The observation equation described, for example, the observed relation between age-$x.3$ recruitment, $R_{x,3}$, and age-$x.2$ recruitment, $R_{x,2}$, from the successive return years y and $y - 1$, respectively

$$(3) \qquad \log_e(R_{x,3,y}) = a_t + b\log_e(R_{x,2,y-1}) + v_t$$

This is the same form as eq. 1 except that a_t values can vary by brood year t; the b parameter remains constant. The error term v_t is normally distributed with a variance σ_v^2. The system equation describes how the a_t parameter (Y intercept) changes over time as follows:

$$(4) \qquad a_t = a_{t-1} + \omega_t$$

where ω_t is a normally distributed error term with a mean of zero and variance σ_ω^2. Here, we assumed a random-walk process for the system equation because we had no a priori knowledge of temporal pattern in a_t values. As well, Peterman et al. (2000) showed that a random-walk model performed well at tracking a wide variety of underlying temporal patterns in parameters. We estimated values for a_t via a sequential updating procedure; the b, σ_v^2, and σ_ω^2 were estimated via maximum likelihood (Chatfield 1996). For an in-depth description of methods of parameter estimation for a Kalman filter model, see Peterman et al. (2003).

Unlike eq. 3, we originally investigated a Kalman filter in which both the a and b parameters (Y intercept and slope) varied with time (i.e., $\log_e(R_{x,3,y}) = a_t + b_t\log_e(R_{x,2,y-1}) + v_t$). However, the estimated b_t turned out to be constant for most stocks, whereas a_t usually varied considerably with time. Furthermore, when data were subdivided into shorter time series (e.g., pre-1976 regime shift and post-1976 regime shift) and analyzed using the standard sibling model with constant parameters, the a parameter differed between subsets, but the b parameter did not. Therefore, we allowed only the a parameter to vary in our analysis (eq. 3).

For the Kalman filter model, we calculated annual values for a_t (i.e., filtered values) using only data from the years prior to the year being estimated (Chatfield 1996; de Valpine and Hastings 2002). To estimate the best-fit values for a_t over the entire data set after completing the estimation of all annual filtered a_t values, we also calculated fixed-interval smoothed a_t values (Harvey 1989), which used data from all years to estimate each a_t value. The smoothed a_t values were calculated sequentially backwards in time starting with the final year. The previous year's smoothed estimate (a_{t-1}) was calculated based on the smoothed and filtered estimates of a_t from year t and their variances. This procedure was repeated for each year in the data set. The filtered values reflected more short-term interannual variability in a_t than the smoothed values. Because the smoothed a_t estimates represent the optimal fit to the data (Chatfield 1996; de Valpine and Hastings 2002), we used these values in further analyses, unless stated otherwise. To permit comparisons among stocks with different mean ages-at-maturity, we standardized the time series of a_t estimates for each stock and age stanza using each stock's respective mean a_t value and variance.

Model evaluation: retrospective analysis

We used a retrospective analysis to compare the forecasts of the standard sibling model and its Kalman filter version. This method evaluates how models would have performed in actual practice; it uses only a subset of the data (e.g., the first n years) to estimate model parameters and forecast the dependent variable in year $n + 1$. This procedure is repeated iteratively for each year of data using knowledge of only previous years' data to estimate model parameters and make forecasts. Other approaches (e.g., cross-validation and bootstrapping; Shao 1993) were either difficult or inappropriate to use in this case owing to the sequential nature of calculations for fitting the Kalman filter model; furthermore, their performance with Kalman filter models has not been evaluated.

Forecasts of abundance of recruits were calculated from the natural logarithm of abundances (eq. 3) using the standard adjustment for back-transformation bias

$$(5) \qquad R_{pred} = R_{nonadjusted} + \sigma_2/2$$

where R_{pred} is predicted recruitment after bias correction, $R_{nonadjusted}$ is the predicted recruitment prior to bias correction (e.g., $\exp(\log_e R_{x,3,y})$), and σ^2 is the residual variance of the forecasting model (Beauchamp and Olson 1973). Our two performance measures for comparing the standard sibling and Kalman filter models were (*i*) mean-squared error (MSE) (i.e., $\Sigma(R_{pred} - R_{obs})^2/N$, where R_{obs} is observed recruitment and N is the number of years of forecasted recruits), and (*ii*) mean percent bias summed over each time series (i.e., $[(\Sigma R_{pred} - \Sigma R_{obs})/\Sigma R_{obs}] \times 100$). We used the latter measure of bias instead of the commonly used annual mean percent error because the annual mean percent error has a positive bias when the observed recruitment has a large random component. For example, when the coefficient of variation of the residual forecasting error is 0.5, the mean percent error calculated from each observation separately will be positively biased by 25% (B. Pyper, S.P. Cramer & Associates Inc., 600 NW Fariss Road, Gresham, OR 97030, USA, personal communication).

Spatial covariation among stocks in the a_t parameter of the sibling model

We identified the spatial scale of physical and biological processes driving changes in a_t by estimating the spatial scale across which a_t values were positively correlated among stocks. We examined four hypotheses for the spatial scale of

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these processes. First, local-scale (i.e., stock-specific) mechanisms may be responsible for variations in a_t, resulting in no correlation of a_t among stocks. Second, regional-scale mechanisms may be responsible for variations in a_t, resulting in correlations among stocks within regions (e.g., Bristol Bay, Alaska) but not among two or more of our eight regions (e.g., between Bristol Bay and Kodiak, Alaska). Third, large-scale mechanisms may be responsible for variations in a_t, resulting in correlations among stocks within a region as well as among regions. For this hypothesis, we defined large scale as the spatial scale at which stocks from several regions can be influenced simultaneously (e.g., the area of overlap in ocean distribution for sockeye stocks from across British Columbia and Alaska; French et al. 1976). Fourth, a combination of these mechanisms may act at various scales, resulting in different correlations within and among regions.

To examine these hypotheses, we calculated Pearson product-moment correlation coefficients between the a_t series for each pair of stocks using the maximum number of years possible for each paired comparison. Mean correlation coefficients were calculated both within and among regions using Fisher's z transform of each correlation coefficient to normalize the distribution prior to calculating the mean (Zar 1999). We were interested in the general overall pattern of correlations among stocks within and among regions rather than in particular pairwise comparisons.

Correlations with physical and biological variables

Using correlation analysis, we then explored physical and biological factors that might be indirectly associated with changes in the a_t parameter of sibling models through changes in oceanographic conditions that affect body growth rates, for instance. Unfortunately, there is no long-term data series for marine food supply for salmon or size-selective predation over the decades covered by our data to test detailed hypotheses about environmental mechanisms; Ocean Station P zooplankton data were collected only up through 1980. We therefore used various surrogates of ocean conditions. Because we found evidence for trends in a_t values correlated among stocks over wide areas (see Results below), we only examined physical and biological factors that exhibit positive covariation across reasonably large spatial scales. This reduced the chance of spurious correlations between the a_t parameter of sibling models and physical and biological factors.

The first large-scale physical factor was winter mean Pacific Decadal Oscillation (PDO), an index of ocean-basin-wide changes in climate (Mantua et al. 1997) (available from the Joint Institute for the Study of Atmosphere and Ocean, University of Washington, Seattle, Washington; URL: http://jisao.washington.edu/pdo/PDO.latest). The PDO is the first principal component of the mean monthly sea-surface temperature (SST) anomalies across the North Pacific Ocean poleward of 20°N (Mantua et al. 1997); those authors suggested that positive deviations in PDO correlate with increased phytoplankton and zooplankton productivity. The second physical factor was deviation from the winter mean SST in the region where sockeye salmon from different stocks in the northeastern Pacific overlap in the Gulf of Alaska, which was an area enclosing the line of 45°N from 170 to 150°W in the south, the line of 55°N from 155 to 140°W in the north, the point 50°N, 175°W in the west, and the point 50°N, 145°W in the east (Pyper and Peterman 1999). We used monthly SST (degrees Celsius) on a 5° × 5° longitude–latitude grid across this area (D. Cayan and L. Riddle, Climate Research Division, 9500 Gilman Dr., Scripps Institute of Oceanography, La Jolla, CA 92093, USA, personal communication; i.e., the same data as Pyper and Peterman 1999). Mean winter SST deviations were calculated by subtracting the long-term mean SST for 1947–1997 from the SST for each grid cell and month and then averaging across winter months (November–February). SST may directly reflect changes in temperature-dependent physiological processes. Winter SST may also indirectly indicate ocean conditions associated with altered prey or predator abundances and distributions because climatic forcing during the winter influences the subsequent spring and summer ocean productivity (Brodeur and Ware 1992).

In addition to physical factors, biological factors that affect or reflect altered growth rates of body size have been used to explain age-at-maturity schedules (Bigler et al. 1996; Pyper et al. 1999). Therefore, we also estimated correlations between sibling-model parameters and the following biological factors: (*i*) the natural logarithm of total abundance of sockeye salmon recruits in all British Columbia and Alaska stocks, (*ii*) the natural logarithm of abundance of Bristol Bay sockeye salmon recruits (used for a separate analysis of only Bristol Bay stocks because these stocks have common migratory patterns and may experience more competition from stocks within Bristol Bay than from stocks from other regions in British Columbia and Alaska), and (*iii*) the mean body size of age-x.2 female sockeye salmon recruits, which were only available for Bristol Bay stocks (Pyper et al. 1999). The first two factors, abundances of conspecifics, reflect competition for limited food supplies (Bigler et al. 1996; Kaeriyama 1998), which affects body size and growth-dependent maturity schedules. For example, Peterman (1984) estimated that age-specific body weight at maturity for sockeye salmon in British Columbia decreased by 10%–22% when abundance of conspecifics was high during early ocean life. We used natural logarithms of abundances, which normalized residual errors for regressions. The third factor, body size of recruits, may reflect competition due to density-dependent growth in the ocean. Body size during the penultimate year of ocean life when the maturation process is initiated was not available from back-calculating from scales or any other source. We therefore used age- and stock-specific body size at maturity as an indirect index of body size during the prior ocean residence period. We used the mean mideye to fork length of age-x.2 female spawners (Pyper et al. 1999) because body sizes of age-x.3 female spawners in year y are of course unknown when forecasting age-x.3 recruitment in year y.

In the correlation analysis, time series of sibling-model a_t values were aligned with data on physical and biological variables at a variety of time lags, depending on various hypotheses about the period of ocean residence when these variables are most critical for salmon growth and maturation. Environmentally induced changes in age-at-maturity appear to occur within the first 2 years of ocean residence (Peterman 1985; Pyper et al. 1999). However, marine growth, which is associated with subsequent age-at-maturity

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(Bigler et al. 1996; Pyper et al. 1999), appears to be influenced by environmental conditions at various ocean ages. For instance, Rogers and Ruggerone (1993) found that growth increments from scale analyses were correlated with environmental conditions during the first and second years of ocean life for one sockeye salmon stock (Nushagak, Alaska). In contrast, LaLanne (1971) and Pyper et al. (1999) suggested that conditions nearer to the time of return migration have the largest influence on growth and final adult body size (penultimate and ultimate year of ocean life). For fish spending two winters in the ocean (age *x*.2), these periods suggested by different authors will overlap (e.g., the second year of ocean residence is equivalent to the penultimate year). Furthermore, Ruggerone et al. (2003) found that density-dependent interactions between Alaskan pink (*Oncorhynchus gorbuscha*) and sockeye salmon during the second and third years of ocean life (OEY + 1 and OEY + 2, where OEY is ocean-entry year) were critical in determining body size at maturity. Therefore, we first aligned a_t series from sibling models with physical conditions and abundances of sockeye salmon recruits that returned during the second year of ocean life (i.e., the abundance of recruits in the penultimate year for age-*x*.2 fish). We also examined correlations between a_t values and both physical factors and abundances of sockeye salmon recruits aligned by earlier ages (OEY) and later ages (OEY + 2 and OEY + 3) to include factors influencing age-at-maturity and growth at different periods of ocean life. Only a small proportion of the total abundance of recruits return after more than three winters in the ocean (average of <1% for stocks considered here); therefore, older age-classes and later alignments were not considered.

Autocorrelations within each time series of explanatory variables and a_t values increased the chance of incorrectly finding a significant correlation. To reduce this bias, we used the modified Chelton method suggested by Pyper and Peterman (1998) to adjust the degrees of freedom for the hypothesis tests in correlation analyses. Although autocorrelations of some series of a_t values were larger than the range of time series previously simulated by Pyper and Peterman (1998) (>0.9), biases in type I error rates were low for this method even when autocorrelation was 0.9 (the simulated type I error rates were <0.07 when the true type I error was 0.05). Hypothesis testing in the correlation analysis with environmental variables was appropriate because the assumption that variables are bivariate-normally distributed was met.

We calculated the probability P of finding the observed number of significant correlations between a_t values and explanatory variables by chance from a binomial distribution and compared this with the number of significant correlations observed at $\alpha = 0.05$. Only those stocks for which a_t varied over time were included in the analysis that explored various explanatory variables.

Multiple regression

The combined influence of physical factors (SST and PDO) and biological factors (sockeye salmon abundances and age-specific body size at maturity) on temporal variability in a_t was estimated in multiple regressions for each stock individually:

$$(6) \qquad a_{i,t} = c_{i,0} + c_{i,1}(E_1)_{t-x+1} + c_{i,2}(E_2)_{t-x+1} + \ldots + \varepsilon_{i,t}$$

where E_1, E_2,... are physical and biological variables experienced during ocean residence in year $t + x + 1$ (OEY + 1), t is brood year, x is the freshwater age, $c_{i,0}$, $c_{i,1}$, $c_{i,2}$, ... are constants for each stock i, and $\varepsilon_{i,t}$ is a normally distributed error term with variance $\sigma^2_{\varepsilon,i}$.

The assumptions of normality and constant variance were met in this regression model, but the errors were not independent of each other. Therefore, we also separately fit another multiple regression model that accounted for autocorrelation in the residuals of model 6 using an autoregressive term of lag 1 (i.e., an AR(1) model). We did this because Bence (1995) showed that if such autocorrelation is ignored, confidence intervals around the parameters might be underestimated, resulting in type I errors (i.e., including a parameter in the model when the coefficient is not actually significantly different from zero). The model form was the same as the standard multiple linear regression model (eq. 6) except the error term ε_t took the form

$$(7) \qquad \varepsilon_t = \rho\varepsilon_{t-1} + \Phi_t$$

where ε_t are autocorrelated residuals of the linear regression, ρ is the lag-1 autoregressive coefficient, and Φ_t is a normally distributed random-error term.

We used stepwise regressions to add environmental variables to the models (eq. 6) that could explain a significant amount of additional variance in a_t beyond that explained by previously selected variables for each stock. There was no evidence for curvilinear relations between a_t values and environmental variables.

Results

Kalman filter

The majority of sockeye salmon stocks that we examined showed evidence for substantial increasing temporal trends in the a_t values of sibling models (e.g., Naknek River, Alaska, and Skeena River, British Columbia, stocks; Fig. 3). Temporal variability existed in the filtered a_t values for all time series, and most stocks also showed variability over time in the smoothed a_t values (20 out of 24 for the age-1.*z* stanza (Fig. 4), 13 out of 18 for the age-2.*z* stanza (Fig. 5)). A few stocks and age stanzas showed no trend in smoothed a_t (horizontal lines in Figs. 4 and 5) because in those cases, all of the variance was attributed to observation error by the Kalman filter's estimation procedure and none to the systematic process error. Smoothed a_t values were larger than filtered a_t values for a given brood year for many stocks (e.g., Fig. 3) because smoothed estimates a_t were based on the weighted average of the smoothed estimate a_{t+1} and the filtered estimate a_t. When filtered a_t increased over time, as was typically the case, this tended to produce smoothed values that were larger than filtered values. By showing the smoothed a_t values in standardized units (mean equal to 0 and standard deviation equal to 1) and grouping them according to region (Figs. 4 and 5), the similarity in increasing trends over time is evident for most stocks. These temporal trends reflect increasing numbers of fish maturing at later ages for a given abundance maturing at the preceding age.

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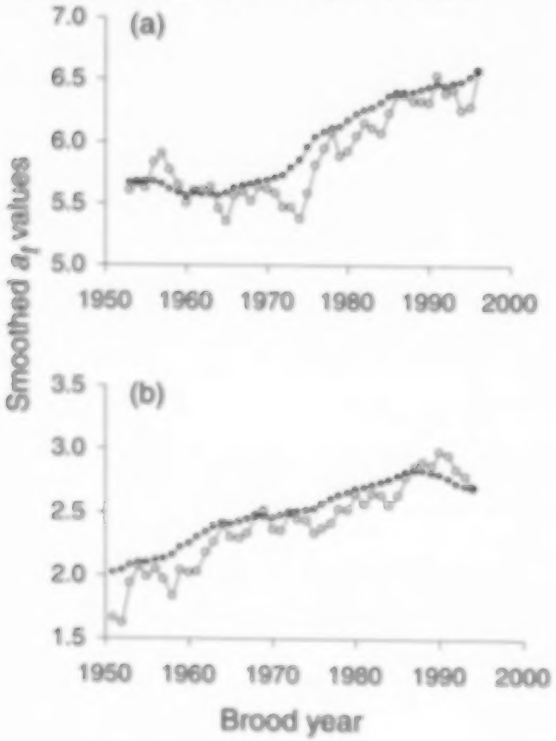

Fig. 3. Kalman filter estimates of the Y intercept for the age-1.z sibling model (i.e., the a_t parameter) for two example sockeye salmon stocks, (*a*) Naknek River, Alaska, and (*b*) Skeena River, British Columbia, as a function of brood year. Smoothed a_t values (squares) and filtered a_t values (circles) are shown.

Model evaluation: retrospective analysis

Our retrospective analyses showed that although the standard sibling model was still best in most stocks, there were many instances in which the Kalman filter model improved forecasts of recruits. Specifically, in 29% of the stocks for the age-1.z stanza and 39% for the age-2.z stanza, the Kalman filter model (which assumed time-varying a_t values) had a smaller MSE of forecasts than the standard sibling model (which assumed a constant a_t). That is, the ratio of the Kalman filter model MSE to the standard sibling model MSE was less than 1.0 for these particular stocks (Fig. 6). Nevertheless, the MSEs of the Kalman filter models were much greater than those of the standard sibling models in many other stocks (Fig. 6).

The ratios of the MSEs from the Kalman filter models to the MSEs from the standard sibling models differed among regions. For example, these ratios were lower for Bristol Bay stocks compared with British Columbia stocks and the other Alaska stocks (Fig. 6). Among Bristol Bay stocks, the MSEs from the Kalman filter models were lower than the MSEs from the standard sibling models for 63% of stocks for the age-1.z stanza and 38% of stocks for the age-2.z stanza. Time series were also longer for the Bristol Bay stocks compared with most stocks from other regions (Table 1). The duration of time series was negatively correlated with the ratios of the MSEs for the Kalman filter models to the MSEs of the standard sibling models, but only for the age-1.z stanza ($r^2 = 0.72$, $P < 0.01$ for the age-1.z stanza; $r^2 = 0.28$, $P > 0.1$ for the age-2.z stanza). Stocks with longer time series were better fit by the Kalman filter models than the standard sibling models owing to increases over time in forecasting errors for the standard models for some stocks.

Over the long term, the mean percent bias was closer to zero for the Kalman filter models than the standard sibling models for most stocks (54% for the age-1.z stanza, 94% for the age-2.z stanza) (Figs. 7 and 8, respectively). One stock, Nelson River, showed a substantially higher positive bias than the other stocks for both the Kalman filter and standard sibling models for the age-1.z stanza (Fig. 7) and for the standard sibling model for the age-2.z stanza (Fig. 8). For this stock, large forecasting errors occurred in 1987 owing to high age-1.2 recruitment in 1986 followed by anomalously low age-1.3 recruitment in 1987. This 1 year of high forecasting error contributed strongly to the mean percent bias for that stock because of the short duration of the data set (14 years).

Spatial covariation of the sibling-model a_t values among stocks

The time series of smoothed a_t values showed strong positive correlations both within and among regions (Figs. 9 and 10). Positive covariation was apparent across both regional and ocean-basin scales, the latter indicated by correlations among British Columbia and Bristol Bay, Alaska, stocks, for example. The mean correlation coefficient was higher for comparisons of stocks within regions than for comparisons among regions for both the age-1.z ($\bar{r}_{\text{within regions}} = 0.85$, $\bar{r}_{\text{among regions}} = 0.63$) and age-2.$z$ ($\bar{r}_{\text{within regions}} = 0.85$, $\bar{r}_{\text{among regions}} = 0.56$) cases. Correlations among smoothed a_t values may be inflated owing to autocorrelation within each time series; however, this cannot explain the observed differences in correlations within and among regions. The filtered a_t values showed similar patterns of covariation with somewhat lower magnitude for both the age-1.z ($\bar{r}_{\text{within regions}} = 0.62$, $\bar{r}_{\text{among regions}} = 0.40$) and age-2.$z$ ($\bar{r}_{\text{within regions}} = 0.75$, $\bar{r}_{\text{among regions}} = 0.50$) cases.

One stock, Black Lake, Alaska, showed considerable differences between its stock-specific trend in a_t for the age-1.z stanza and both the ocean-basin-scale and regional-scale patterns that were common to most other sockeye salmon stocks (Fig. 9). This trend in a_t was highly negatively correlated ($r < -0.5$) with most other stocks. Note that a_t values from Black Lake extend from 1918 to 1994 (Fig. 4, top right), although most correlations in Fig. 9 were computed for only the latter half of the time series (post-1950) when recruitment data for other stocks became available. In contrast with the increasing values observed in most stocks since 1965, a_t values decreased for Black Lake during this period.

Compared with the standard sibling models, the Kalman filter models were better able to distinguish trends in the natural logarithm of age-specific recruitment that are shared among stocks within and among regions. The time-varying estimates of smoothed a_t from the Kalman filter model showed stronger covariation among stocks, both within re-

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Fig. 4. Annual standardized Y intercept (i.e., the smoothed a_t parameter) for the age-1.z sibling model (i.e., fish that spent one winter in fresh water) for Alaska and British Columbia sockeye salmon stocks as a function of brood year t. Graphs are arranged roughly from northern regions at the top left to southern regions at the bottom right. Each line represents the a_t series for one stock. Note the different time periods covered for each stock, especially those for Chignik and Black Lake stocks in the Chignik area, which are over twice as long as the periods for other stocks.

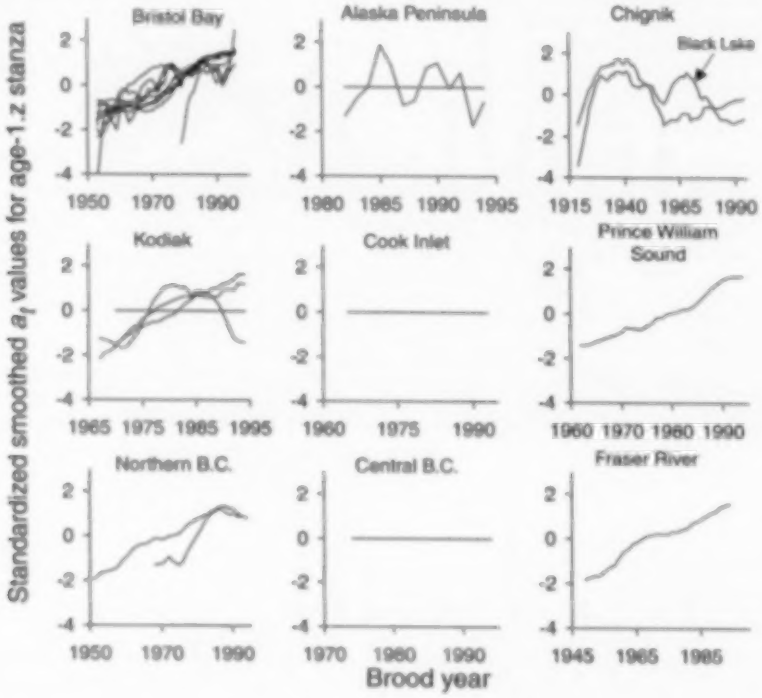

Fig. 5. Annual standardized Y intercept (i.e., the smoothed a_t parameter) for the age-2.z sibling model (i.e., fish that spent two winters in fresh water) for Alaska and British Columbia sockeye salmon stocks as a function of brood year t. Graphs are arranged roughly from northern regions at the top left to southern regions at the bottom right. Each line represents the a_t series for one stock, except for the horizontal lines for Bristol Bay and Kodiak, which apply to three and two stocks, respectively. Note the different periods covered for each stock.

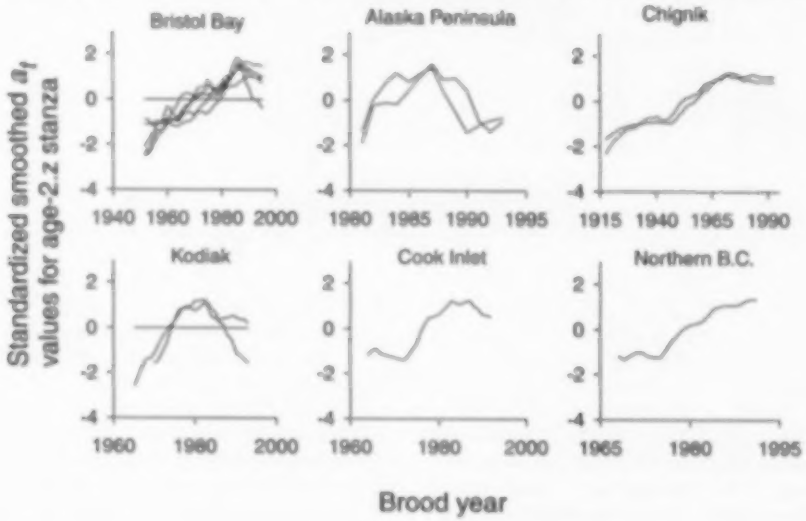

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Fig. 6. Ratios of the mean-squared errors (MSEs) of forecasts from the Kalman filter model to the MSEs of forecasts from the standard sibling model for each sockeye salmon stock. Solid bars represent the age-1.z stanza and open bars represent the age-2.z stanza. Forecasts were produced by a retrospective analysis of 24 stocks across British Columbia and Alaska. Sufficient age-2.z data were not available for six stocks (Pitt River, Long Lake, Skeena River, Copper River, Nushagak, and Nuyakuk). The broken line at a ratio of 1.0 shows where the MSE of the Kalman filter's forecasts is equal to that of the standard sibling model.

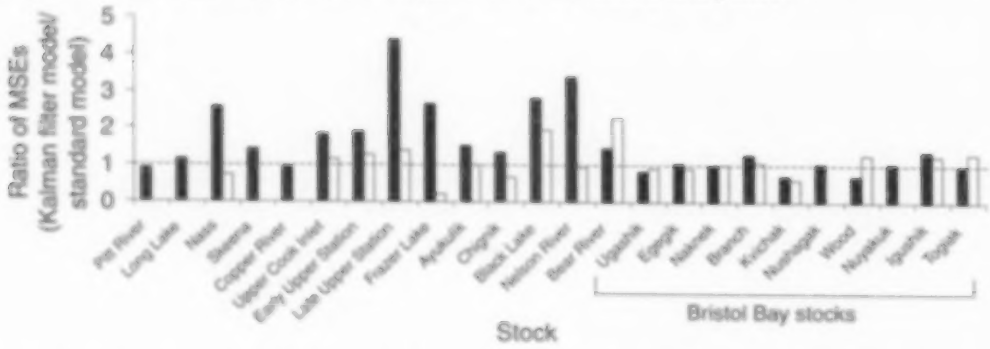


Fig. 7. Mean percent bias of forecasts for the Kalman filter model (solid bars) and the standard sibling model (open bars) from a retrospective analysis of age-1.z recruits for 24 stocks of sockeye salmon across British Columbia and Alaska. The asterisk (*) shows that the mean percent bias for Nelson River was off the scale at 598% and 364% for the Kalman filter and standard sibling models, respectively.

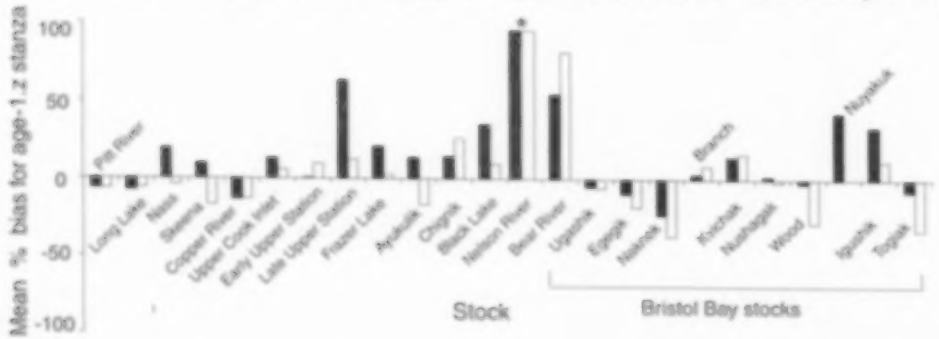
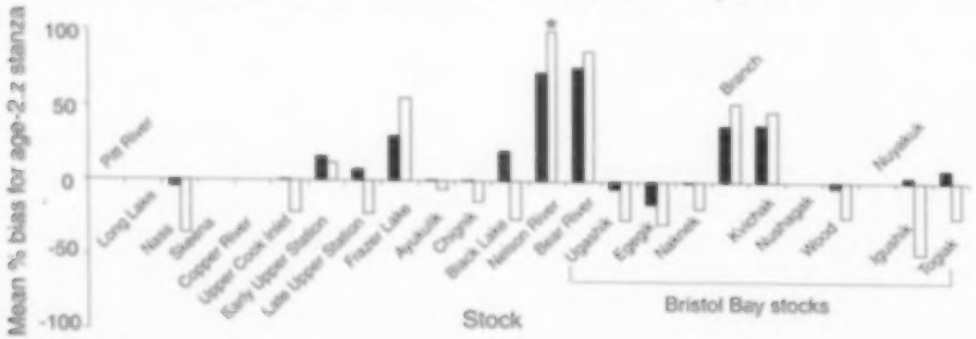


Fig. 8. Mean percent bias of forecasts for the Kalman filter model (solid bars) and the standard sibling model (open bars) from a retrospective analysis of age-2.z recruits for 18 stocks of sockeye salmon across British Columbia and Alaska. The asterisk (*) shows that the mean percent bias for Nelson River was off the scale at 144% for the standard sibling model.



gions and among regions, than the residuals from the standard sibling model (eq. 1) for both the age-1.z and age-2.z stanzas (Fig. 11). This suggests that a_i values capture more of the systematic trends in the sibling relation shared among stocks than residuals from the standard sibling model.

Correlations with physical and biological variables

We found a preponderance of significant positive correlations between a_i values and each of PDO, SST in the Gulf of Alaska, total sockeye salmon abundances, and Bristol Bay sockeye salmon abundances when time series were aligned

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Fig. 9. Correlation matrix of smoothed a_t values for the age-1.z sibling model as estimated by the Kalman filter model for sockeye salmon stocks across British Columbia and Alaska. Stocks with constant a_t values were excluded from the analysis. AP denotes the region of the Alaskan Peninsula, PWS denotes the region of Prince William Sound, and BC denotes British Columbia.

			Bristol Bay										AP	Chignik		Kodiak			PWS	BC	
	Stock	Region	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	Wood	Bristol Bay																			
2	Ugashik	Bristol Bay	0.71																		
3	Togiak	Bristol Bay	0.84	0.67																	
4	Naknek	Bristol Bay	0.82	0.97	0.81																
5	Kvichak	Bristol Bay	0.84	0.97	0.79	0.99															
6	Igushik	Bristol Bay	0.91	0.59	0.73	0.67	0.73														
7	Egegik	Bristol Bay	0.87	0.93	0.81	0.96	0.99	0.76													
8	Branch	Bristol Bay	0.89	0.94	0.80	0.98	0.99	0.77	0.99												
9	Nuyakuk	Bristol Bay	0.90	0.15	0.70	0.45	0.59	0.83	0.76	0.64											
10	Nushagak	Bristol Bay	0.44	0.88	0.59	0.89	0.94	0.67	0.88	0.82	-0.88										
11	Bear River	Alaska Pen. (AP)	0.05	0.12	0.21	0.12	0.22	0.50	0.10	-0.08	-1.00	0.04									
12	Black Lake	Chignik	-0.55	-0.94	-0.51	-0.88	-0.87	-0.49	-0.78	-0.83	0.15	-0.93	-0.35								
13	Chignik Lake	Chignik	0.47	0.80	0.61	0.82	0.76	0.21	0.72	0.73	-0.07	0.62	-0.01	0.44							
14	Frazer Lake	Kodiak	0.73	0.98	0.48	0.97	0.98	0.69	0.99	0.95	-0.34	0.80	-0.02	-0.94	0.94						
15	Late Upper Station	Kodiak	0.05	0.28	0.51	0.36	0.30	0.47	0.21	0.40	-0.75	-0.44	0.18	-0.42	0.24	0.10					
16	Ayakulik River	Kodiak	0.87	0.94	0.53	0.97	0.95	0.80	0.90	0.98	-0.11	0.66	-0.20	-0.97	0.87	0.92	0.38				
17	Copper River	Pr.Wm.Sd.(PWS)	0.81	0.96	0.63	0.95	0.96	0.74	0.98	0.95	0.51	0.67	-0.03	-0.92	0.94	0.98	0.00	0.88			
18	Skeena River	Northern BC (BC)	0.92	0.78	0.85	0.88	0.91	0.85	0.94	0.94	0.88	0.70	0.49	-0.64	0.28	0.89	0.57	0.90	0.90		
19	Nass River	Northern BC (BC)	0.50	0.96	0.50	0.93	0.96	0.66	0.96	0.93	-0.77	0.97	0.44	-0.93	0.82	0.93	0.55	0.88	0.88	0.97	
20	Pitt	Fraser River (BC)	0.93	0.76	0.81	0.85	0.89	0.84	0.95	0.91	0.95	0.76	-0.07	-0.60	-0.01	0.98	-0.05	0.85	0.99	0.97	0.90

correlation coefficient > 0.5
correlation coefficient >0 and < 0.5
correlation coefficient <0

Fig. 10. Correlation matrix of smoothed a_t values for the age-2.z sibling model as estimated by the Kalman filter model for sockeye salmon stocks across British Columbia and Alaska. Stocks with constant a_t values were excluded from the analysis. AP denotes the region of the Alaskan Peninsula, CI denotes the region of Cook Inlet, and BC denotes British Columbia.

			Bristol Bay					AP		Chignik		Kodiak		CI
	Stock	Region	1	2	3	4	5	6	7	8	9	10	11	12
1	Wood	Bristol Bay												
2	Ugashik	Bristol Bay	0.74											
3	Togiak	Bristol Bay	0.93	0.91										
4	Naknek	Bristol Bay	0.82	0.73	0.87									
5	Egegik	Bristol Bay	0.72	0.94	0.89	0.64								
6	Nelson River	Alaska Pen. (AP)	-0.48	0.26	0.56	0.87	0.04							
7	Bear River	Alaska Pen. (AP)	0.07	0.76	0.86	0.70	0.50	0.64						
8	Black Lake	Chignik	0.90	0.46	0.75	0.77	0.38	0.13	-0.05					
9	Chignik Lake	Chignik	0.96	0.64	0.87	0.86	0.56	0.62	0.09	0.97				
10	Frazer Lake	Kodiak	0.63	0.83	0.69	0.65	0.55	-0.06	-0.23	-0.06	0.61			
11	Early Upper Stuart	Kodiak	-0.15	0.21	-0.03	0.43	-0.12	0.52	0.09	-0.04	0.17	0.75		
12	Upper Cook Inlet	Cook Inlet (CI)	0.77	0.94	0.84	0.69	0.86	0.90	0.55	-0.41	0.29	0.76	0.53	
13	Nass River	Northern BC (BC)	0.86	0.95	0.93	0.61	0.97	-0.04	0.54	-0.84	-0.30	0.63	0.16	0.91

correlation coefficient >0.5
correlation coefficient >0 and <0.5
correlation coefficient <0

by OEY + 1 (Table 2). These positive correlations, which were significant after taking autocorrelation into account, were found in 61% of the analyses of pairs of time series for age 1.z and 59% for age 2.z, many more than would be expected by chance alone if the correlations were in fact zero (Table 2). In particular, as PDO, SST, total sockeye salmon abundances, and Bristol Bay sockeye abundances increased, a larger number of fish tended to return for a given recruitment at the preceding age in the previous year (i.e., a_t increased); this was true for both age stanzas (Table 2). Higher values of the physical variables (PDO and SST) represent higher temperatures and also indirectly indicate higher phytoplankton and zooplankton productivity (Mantua et al. 1997). The biological variables, total and Bristol Bay sockeye abundances, are an index of competition among stocks. Negative correlations were infrequent for the correlations between a_t and both the physical and biological variables mentioned above (PDO, SST, and sockeye abundances) (Table 2). Similar significant positive correlations were found for PDO, SST, and sockeye abundances when the alignment of data series was changed to OEY, OEY + 2, or OEY + 3. One exception was that most correlations between PDO and

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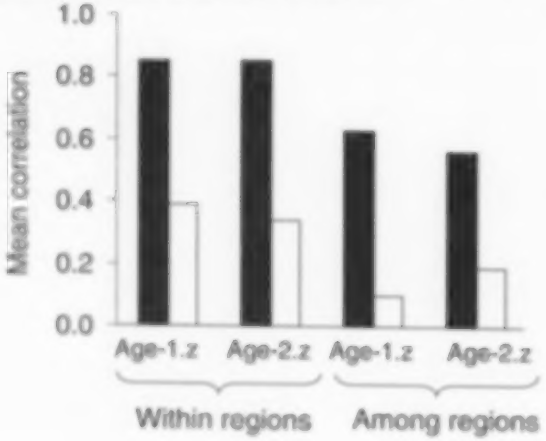
Fig. 11. Means of correlations between pairs of sockeye salmon stocks in their time series of smoothed Kalman filter a_t values (solid bars) as well as between their residuals from standard sibling models (open bars) within and among the eight regions. Both age-1.*z* and age-2.*z* stanzas are shown.



parameters of sibling models were not statistically significant ($P > 0.05$) when aligned by OEY + 3 (i.e., fewer cases were significant than expected by chance alone).

In contrast, we found significant negative correlations between a_t and body size of age-1.2 recruits in three of seven Bristol Bay stocks for the age-1.*z* stanza (Table 2, bottom). For that age stanza, there were more significant negative correlations than expected by chance alone if there were in fact no correlation ($P < 0.001$). In other words, as the body size of age-1.2 recruits declined, a larger number of fish tended to return at age 1.3 for a given abundance at age 1.2. There were no significant positive correlations for these comparisons. For fish that spent two winters in fresh water (age-2.*z* stanza), no significant correlations existed between a_t values and body size of age-2.2 recruits (Table 2, bottom). The exclusion of some stocks because of stationary a_t values probably did not bias our results because only a small number of stocks were excluded from this analysis (four out of 24 and five out of 18 stocks for the age-1.*z* and age-2.*z* stanzas, respectively).

Multiple regression

To obtain further information on the influence of each environmental variable on a_t, we performed a multiple linear regression aligning data for independent variables by OEY + 1. The natural logarithm of total sockeye salmon abundance explained a significant portion of the variability in a_t in more time series than any other environmental variable (29 out of 33 time series) (Table 3). When modelling a_t values as a function of physical and biological variables, SST was included as an explanatory variable in almost half of these cases (17 out of 33). PDO and Bristol Bay sockeye salmon abundances were only included in a small number of models and therefore could explain variability in a_t beyond that explained by total sockeye salmon abundance and SST in only a small portion of the stocks. However, multicollinearity among some of these environmental variables (Table 4) cre-

Table 2. Summary of correlations between smoothed Kalman filter a_t values for the sibling model and time series of physical and biological variables.

Physical or biological variable	Age-class stanza	*N*	No. of significant positive correlations	Median *r* for significant positive correlations (range)	P_{1+}	No. of significant negative correlations	Median *r* for significant negative correlations (range)	P_{1-}
log$_e$(total sockeye abundance)	1.*z*	20	17	0.65 (0.54, 0.76)	<0.001	1	–0.64	>0.2
	2.*z*	13	10	0.62 (0.44, 0.72)	<0.001	0	—	>0.5
log$_e$(Bristol Bay sockeye abundance)	1.*z*	10	7	0.56 (0.35, 0.58)	<0.001	0	—	>0.5
	2.*z*	5	5	0.47 (0.39, 0.59)	<0.001	0	—	>0.5
PDO	1.*z*	20	10	0.45 (0.38, 0.50)	<0.001	0	—	>0.5
	2.*z*	13	6	0.45 (0.37, 0.53)	<0.001	1	–0.39	>0.2
SST	1.*z*	20	9	0.46 (0.33, 0.54)	<0.001	3	–0.47 (–0.59, –0.41)	0.013
	2.*z*	13	5	0.49 (0.37, 0.58)	<0.001	0	—	>0.5
Body size of Bristol Bay age-1.2 recruits	1.*z*	7	0	—	>0.5	3	–0.42 (–0.51, –0.29)	<0.001
	2.*z*	5	0	—	>0.5	0	—	>0.5

Note: Physical or biological variable and age-class stanza describe the variables in each pairwise correlation for which a_t values were used; PDO is the Pacific Decadal Oscillation; SST is sea-surface temperature; age-class stanzas 1.*z* and 2.*z* represent the relation between age-1.2 and age-1.3 fish and between age-2.2 and age-2.3 fish, respectively; *N* is the total number of correlations calculated (corresponding to the number of stocks analyzed). The number of significant positive correlations at the $\alpha = 0.05$ level and the median and range for these correlations (r) are shown; P_{1+} is the probability of finding that number of significant positive correlations by chance alone, calculated from the binomial distribution. Similarly, the table shows the number of significant negative correlations at the $\alpha = 0.05$ level, the median and range for these correlations, and the probability of finding that number of significant negative correlations by chance alone, P_{1-}.

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Table 3. Results of multiple linear regressions of Kalman filter a_t values (Y intercept) for the sibling models on physical and biological variables for sockeye salmon stocks in British Columbia and Alaska.

	Fraction of stocks for which each explanatory variable is included in the stepwise procedure for the regression					
Age-class stanza	$\log_e$(total sockeye abundance)	$\log_e$(Bristol Bay sockeye abundance)	SST	PDO	Mean adjusted r^2 (range)	Mean lag 1 autocorrelation coefficient of residuals (range)
1.*z*	18/20	1/10	12/20	0/20	0.48 (0.14, 0.64)	0.66 (0.01, 0.87)
2.*z*	11/13	0/5	5/13	2/13	0.38 (0.08, 0.67)	0.72 (0.16, 0.95)
Total cases	29/33	1/15	17/33	2/33	0.45 (0.08, 0.82)	0.69 (0.01, 0.94)

Note: The fraction of stocks is listed for which each explanatory variable was included in a stepwise add-in procedure ($\alpha \leq 0.05$ for inclusion). SST is the deviation in sea-surface temperature from the winter mean in the Gulf of Alaska, and PDO is the Pacific Decadal Oscillation index.

ates confounding of interpretation of these results. More importantly, autocorrelation in the residuals (Table 3) prompted us to also fit a multiple regression (eq. 6) that included an autoregressive lag-1-year error term (eq. 7). Once that autocorrelation was accounted for, none of the environmental variables was consistently significant in the model, often resulting in the null model (i.e., a model containing the Y intercept only).

Discussion

Many North American sockeye salmon stocks show increases in a_t parameters of their sibling models over the last 40 years. These changes reflect increases in the number of older fish maturing and recruiting relative to younger ones from the same brood class and ocean-entry year. In other words, more adults have returned recently at ages 1.3 and 2.3 for a given abundance of recruits of ages 1.2 and 2.2, respectively. For example, for the age-1.2 to age-1.3 stanza for the Kvichak stock (Bristol Bay), the a_t values increased from 3.5 in 1952 to 4.3 in 1996, reflecting a change in the ratio of age-1.3 to age-1.2 recruitment from 0.7:1 in 1952 to 3.2:1 in 1996. These increases in a_t values were qualitatively similar to increases in mean age-at-maturity over the same time period for 31 sockeye salmon stocks in British Columbia and Alaska (Pyper et al. 1999). Only a few stocks showed little or no evidence of consistent temporal trends in a_t over time.

These results of increasing values of a_t over time for most stocks are unlikely to be a spurious result of errors in estimating escapements. For us to have come to the wrong conclusion about increasing trends in sibling model a_t values, there would have to have been a systematic time trend toward increasingly overestimating the proportion of older fish relative to younger ones in each successive year.

Incorporating temporal variability in the Y intercept (a_t) of the sibling models using a Kalman filter resulted in retrospective forecasts with mean percent biases closer to zero for most stocks compared with using standard sibling models, which assume constant parameters over time. However, the Kalman filter model did not improve the MSE of forecasts of recruitment consistently across all stocks that showed changes in age-specific recruitment over time. Kalman filter models reduced the residual errors from retrospective forecasts for only 29% of the stocks for the age-1.*z* stanza and 39% of the stocks for the age-2.*z* stanza compared with standard sibling models. Nevertheless, Kalman filter models improved forecasts for a higher proportion of Bristol Bay stocks than for the other Alaska plus British Columbia stocks. This was especially true for the measure of bias of forecasts. It is not clear whether this result for Bristol Bay stocks was due to (*i*) a larger change in the a_t parameters in that region, (*ii*) the longer average duration of Bristol Bay sockeye time series compared with other stocks, both of which might favour parameter estimation with the more complex Kalman filter model, or (*iii*) a combination of these factors. Nonetheless, Kalman filter models should be seriously considered for forecasting age-specific recruitment in at least the Bristol Bay region; other regions may or may not benefit from this model in the future as more data accumulate.

The numerous cases of positively biased forecasts from the Kalman filter model, especially for stocks outside Bristol Bay, can be explained by the observation that when age-*x*.2 recruitment was high, this model occasionally greatly overestimated age-*x*.3 recruitment in the subsequent year. This phenomenon was likely due to the annually updated estimates of a_t being substantially altered owing to large outliers in the data. In such cases, the changing a_t may tend to follow the noise in the sibling relation rather than the systematic changes that we hoped to capture.

In addition to improving forecasts for some stocks, Kalman filter models, when compared with standard sibling models, can help to better identify systematic trends in age structure of recruits that are associated with long-term physical and biological processes. Kalman filters do this by reducing the confounding of interpretation resulting from random sources of error independent of these trends. These less-confounded estimates of systematic process variation reflected by a_t values can lead to higher-power tests of mechanisms causing changes in proportional age distributions of sockeye salmon recruits.

Further information about the type of environmental processes that strongly affect changes in age-at-maturity is provided by the relative magnitude of pairwise correlations of a_t series at the regional and ocean-basin scales. The mean correlation of stock-specific smoothed a_t values among stocks at the regional scale (0.85 for both age stanzas) was positive and greater than the mean correlation among stocks at the ocean-basin scale (0.56–0.63, depending on the age stanza). These mean correlations suggest that processes that are most important for changes in stock-specific a_t values are shared among stocks at both regional and ocean-basin scales. The larger mean correlation within regions can be explained by a combination of regional- and ocean-basin-scale processes,

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Table 4. Summary of correlation coefficients among physical and biological variables.

	PDO	SST	$\log_e$(total sockeye abundance)
SST	0.16		
$\log_e$(total sockeye abundance)	0.26	0.32	
$\log_e$(Bristol Bay sockeye abundance)	0.46*	0.17	0.58*

Note: SST is the deviation in sea-surface temperature from the winter mean in the Gulf of Alaska, and PDO is the Pacific Decadal Oscillation index. An asterisk indicates a significant correlation at $\alpha = 0.05$.

whereas the mean correlation among regions reflects only ocean-basin-scale processes.

In contrast, local-scale processes may dominate for a few stocks such as Black Lake, overriding regional or large-scale processes. In that stock, the age-1.2 a_t parameter declined after the 1970s as a result of declines in age-1.3 recruitment, without concurrent declines in age-1.2 recruitment. The unique hydrogeological characteristics of Black Lake may explain its decreasing a_t values over the last 30 years, which are unlike the increasing a_t values generally shown by other stocks in that region. Since the 1960s, Black Lake has experienced substantial reductions in water volume because of erosion of outflow rivers (Ruggerone et al. 2001). Lower water levels have reduced in-lake habitat area and have made upstream migration more arduous, especially for larger adults (Ruggerone et al. 2001). Therefore, larger (and older) recruits may experience higher prespawning mortality before they are enumerated, thereby resulting in fewer age-1.3 recruits compared with age-1.2 recruits and decreased a_t values.

Pyper et al.'s (*1999*) analysis of the spatial scale of covariation in mean age-at-maturity concluded that ocean-basin-scale processes dominate over those acting on age-at-maturity at regional scales. However, in addition, Pyper et al. (*1999*) found substantial stock-specific variation in mean age-at-maturity, whereas we found that stock-specific variations in a_t were small compared with regional and large-scale variations. The difference between the results of these two studies can be explained by the different metrics used. First, the mean age-at-maturity used by Pyper et al. (*1999*) is a weighted average that integrates recruitment over all age-classes from brood classes that entered the ocean in the same year (e.g., ages 1.1, 1.2, 1.3, and 1.4). In contrast, our sibling-model a_t parameter reflects the association between the logarithm of abundances of only two age-classes (e.g., age 1.2 and age 1.3). Therefore, differences at younger (age 1.1) and older (age 1.4) age-classes will not be represented in the a_t values estimated here. Second, mean age-at-maturity is calculated for each brood year and is sensitive to annual anomalies such as extremely high recruitments of specific age-classes, whereas a_t values are calculated using data from all years and reflect longer-term trends in age structure that are normally masked by random interannual variability. Therefore, in addition to long-term trends, mean age-at-maturity will be more likely to reflect patterns at short temporal scales that are often associated with patterns at small spatial scales (Holling 1992) and that are not detected by sibling-model a_t values.

Our results suggest that processes acting at regional as well as ocean-basin spatial scales are mostly responsible for the temporal increases in sibling-model a_t values. The ocean-basin-scale processes may influence fish from different stocks either when they co-occur in the Gulf of Alaska or at other points in their ocean life when they still share large-scale physical or biological conditions. Alternatively, each stock may be independently influenced by separate conditions, which have coincidentally resulted in similar trends in a_t values.

For at least two reasons, it is difficult to attribute particular causal mechanisms to the observed covariation in sibling-model parameters at either regional or ocean-basin scales. First, there is some multicollinearity among the physical and biological explanatory variables as well as autocorrelation in their time series, which precludes convincingly distinguishing the separate influences on sibling-model a_t values of abundance of conspecific competitors, age-specific body size, or ocean temperatures (PDO and SST) and the conditions that the latter indirectly reflect. Specifically, in the multiple regressions, collinearity between total sockeye salmon abundance and PDO means that PDO cannot explain much additional variance in a_t values not already explained by sockeye salmon abundances and vice versa. Second, some unspecified latent variable(s) might directly affect both a_t and one or more of our explanatory variables, coincidentally creating the observed correlations between the latter and a_t. For example, none of the environmental variables was consistently significant in our analyses that assumed a lag-1 autocorrelated residual variation. Third, but less problematic, correlations in a_t values among stocks may cause an underestimate of the frequency of type I errors in the correlation analyses between a_t values and explanatory variables (i.e., resulting in too many significant cases from P values that are too low). However, the P values were well below $\alpha = 0.05$ ($P < 0.001$ for most comparisons), so it is unlikely that this bias will change the interpretation of results.

Nevertheless, recall that the total abundance of sockeye salmon in the Gulf of Alaska was the variable we examined that was most frequently (and positively) associated with a_t in our multiple regressions (29 out of 33 cases). If that abundance of conspecifics is actually the most important explanatory variable for the temporal increases in a_t values, this would be consistent with the large amount of previous research documenting the interaction among increased abundance of conspecifics, reduced density-dependent growth, and delayed maturation of sockeye salmon. For instance, an inverse relation between total abundances of chum salmon (*Oncorhynchus keta*) (or sockeye salmon) and growth during their marine life is well documented based on body size at maturity (Peterman 1984; Kaeriyama and Katsuyama 2001; Ishida et al. 2002), scale analyses (Rogers and Ruggerone 1993; Ruggerone et al. 2002), and stomach contents (Tadokoro et al. 1996; Davis et al. 1998). Such effects of a given abundance of competitors are, of course, influenced by

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oceanographic conditions that affect biological productivity of food for salmon (e.g., Aydin et al. 2000; Kaeriyama et al. 2000). The final link between abundance and a_t values is that relatively small age-specific body size at maturity tends to be associated with late age-at-maturity in several salmon species, including sockeye (Kaeriyama 1998; Pyper et al. 1999). Furthermore, sockeye salmon abundances have increased in the Gulf of Alaska over the previous 30 years (Pyper and Peterman 1999). Given the above linkages among abundance of competitors, growth rate, and age-at-maturity in salmon, the increasing a_t values over time for sibling models reported here are thus consistent with that temporal trend in abundance.

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Spatial hierarchical Bayesian models for stock–recruitment analysis of pink salmon (*Oncorhynchus gorbuscha*)

Zhenming Su, Randall M. Peterman, and Steven L. Haeseker

Abstract: To improve the understanding of effects of environmental factors on spawner-to-recruit survival rates of pink salmon (*Oncorhynchus gorbuscha*), we developed several spatial hierarchical Bayesian models (HBMs). We applied these models to 43 pink salmon stocks in the Northeast Pacific. By using a distance-based, spatially correlated prior distribution for stock-specific parameters, these multistock models explicitly allowed for positive correlation among nearby salmon stocks in their productivities and coefficients of early summer coastal sea surface temperature (SST). To our knowledge, this is the first time that such distance-based, spatial prior probability distributions for parameters have been applied to fisheries problems. We found that the spatial HBMs produce more consistent and precise estimates of effects of SST on productivity than a single-stock approach that estimated parameters for each stock separately. Similar to earlier results using mixed-effects models for the same stocks, we found significant positive effects of SST on survival rates of northern pink salmon stocks, but weaker negative effects of SST on survival rates of southern pink salmon stocks. However, we show a smoother transition in magnitude of effects between these regions.

Résumé : Afin de mieux comprendre les effets des facteurs du milieu sur les taux de survie reproducteurs-recrues du saumon rose (*Oncorhynchus gorbuscha*), nous avons mis au point plusieurs modèles spatiaux hiérarchiques bayésiens (HBMs). Nous avons appliqués ces modèles à 43 stocks de saumons roses du nord-ouest pacifique. En utilisant des distributions a priori basées sur la distance et corrélées spatialement pour les paramètres spécifiques aux stocks, ces modèles multi-stock permettent explicitement une corrélation positive entre les stocks voisins de saumons, en ce qui a trait à leurs productivités et les coefficients de température de surface de la mer (SST) sur la côte en début d'été. C'est à notre connaissance la première fois qu'une telle distribution de probabilité spatiale a priori basée sur les distances des paramètres est utilisée dans une étude sur les poissons. Les HBMs spatiaux produisent des estimations plus concordantes et plus précises des effets de SST sur la productivité qu'une méthodologie qui estime les paramètres séparément pour chaque stock. Comme dans nos résultats obtenus à l'aide de modèles d'effets mixtes sur les mêmes stocks, il y a des effets positifs significatifs de SST sur la survie des stocks plus nordiques de saumons roses et des effets négatifs plus faibles de SST sur la survie des stocks de saumons roses plus au sud. Cependant, nous montrons une transition plus graduelle de l'importance de ces effets ente les deux régions.

[Traduit par la Rédaction]

Introduction

Recruitment of Pacific salmon (*Oncorhynchus* spp.) is characterized by large interannual variation, which creates uncertainties and risks related to conservation and sustainable uses. To reduce these uncertainties and risks, we need to better understand sources of variation in recruitment. For Pacific salmon, stock–recruitment relationships that only use spawner abundance as the independent variable usually explain little of the variation. Therefore, much effort has been directed to taking into account effects of environmental processes on salmon survival rates (Ware and McFarlane 1989; Beamish 1995).

Usually, environment–recruitment analyses have been conducted on single stocks by correlating recruitment with one or more environmental factors (Pearcy 1992; Beamish 1995). However, results obtained from this single-stock approach may be unreliable. Few correlations identified in the past persist when new data are added, indicating that many of them are spurious (Myers 1998). Stock–recruitment data

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Z. Su,[1,2] R.M. Peterman, and S.L. Haeseker.[3] Fisheries Science and Management Research Group, School of Resource and Environmental Management, Simon Fraser University, 8888 University Drive, Burnaby, BC V5A 1S6, Canada.

[1]Corresponding author (e-mail: SUZ@michigan.gov).
[2]Present address: Institute for Fisheries Research, Michigan Department of Natural Resources, 212 Museums Annex Building, 1109 North University Avenue, Ann Arbor, MI 48109-1084, USA.
[3]Present address: USFWS Columbia River Fishery Program Office, 9317 NE Hwy 99, Suite 1, Vancouver, WA 98665, USA.

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sets are usually short, highly variable, and often temporally autocorrelated. Inferences obtained from such data are prone to estimation problems (Walters and Collie 1988).

However, data for multiple nearby stocks are often available. In such cases, previous studies have found that spawner-to-recruit survival rates of nearby salmon stocks are usually positively correlated after within-stock, density-dependent effects have been removed by fitting stock–recruitment relations and calculating residuals (Myers et al. 1997; Peterman et al. 1998; Pyper et al. 2001). Our purpose in this research project was to analyze data from multiple stocks, taking these spatial correlations into account, and to potentially obtain a better understanding of influences of environmental effects on salmon recruitment.

Hierarchical Bayesian modeling, a statistical tool for combining information for data sets with a hierarchical or nested structure, is ideal for this type of data analysis (Gill 2002). Utilizing this approach, we can use data for numerous stocks to improve parameter estimates and their precision for each individual stock.

Hierarchical models are becoming increasingly popular for analyzing complex fisheries data. Hilborn and Liermann (1998) provide a review of hierarchical Bayesian meta-analyses. Myers (2001) gives a comprehensive review of applications of meta-analysis by variance component models and mixed-effects (ME) models for multistock stock–recruitment analyses. Su et al. (2001) and Adkison and Su (2001) apply hierarchical Bayesian models (HBMs) to improve annual escapement estimation from salmon historical spawning stream counts. Other applications of Bayesian or non-Bayesian hierarchical models include analyses of catchabilities for research trawl surveys (Harley and Myers 2001; Millar and Methot 2002), mark–recapture data of Atlantic salmon (*Salmo salar*) (Rivot and Prevost 2002), size-at-age data (Schaalje et al. 2002), a regional metamodel for salmon (Chen and Holtby 2002), and harbor seal (*Phoca vitulina richardsi*) abundance (ver Hoef and Frost 2003). More related to the present paper, Mueter et al. (2002*a*) used an ME model to better understand environmental effects on spawner-to-recruit survival rates of Pacific salmon.

Common to all these analyses is their use of a common population or prior distribution to model possible associations among a collection of parameters across multiple data sets. For example, the productivity parameters of multiple salmon stocks in a region might be similar and may be treated as a random sample drawn from a population of productivity parameters. These parameters are called exchangeable in the sense that their joint distributions are invariant to any possible permutation of their indexes (or locations) and can be treated as independent and identically distributed (iid) given further population parameters (e.g., regional mean value of the productivities of the salmon stocks) (Gelman et al. 2004). Therefore, no temporal or spatial structure is considered by such exchangeable prior distributions.

In this paper, we extend these studies by explicitly incorporating spatial correlation structure in our models. Recent research in epidemiology and geography has demonstrated the importance of explicitly modeling such spatial structure in data (Moura and Migon 2002). We model the spatial correlation by imposing complex dependence structures (i.e., spatially correlated prior distributions) on stock-specific parameters. Such prior distributions allow the models to utilize information from neighboring areas to smooth estimates of parameters for individual stocks (Banerjee et al. 2004).

We first develop spatial HBMs that incorporate spatial autocorrelation in parameters of a generalized Ricker model to help explain variation over time in spawner-to-recruit survival rates. To do this, we adopt a distance-based, conditional autoregressive (CAR) spatial prior distribution for model parameters (Besag et al. 1991). To our knowledge, this is the first time that such distance-based CAR prior probability distributions have been applied to fisheries problems (the only other close example is Hirst et al. (2004), who analyzed cod catches using CAR priors that were not distance-based but instead referred to fixed fishing regions near Norway). We also develop alternative models and compare these with spatial HBMs using the deviance information criterion (DIC), which is analogous to the Akaike information criterion (AIC) but is applicable to hierarchical Bayesian models (Spiegelhalter et al. 2002). We use Markov chain Monte Carlo (MCMC) techniques (Gilks et al. 1996) to carry out the associated computations. Finally, we apply the spatial HBMs to examine the influence of environmental factors (sea surface temperature (SST) here) on survival rates of pink salmon (*Oncorhynchus gorbuscha*) stocks distributed along the west coast of North America. The main difference between our work and that of Mueter et al. (2002*a*) is that we allow for spatial structure of different stocks' parameters to be based in part on the distance between ocean entry points of stocks. This relaxes the more restrictive assumption of Mueter et al. (2002*a*) that the parameters within a given region (e.g., Alaska) were all randomly drawn from a single distribution.

Methods

HBMs are usually specified in a nested manner. We first model the data (spawner-to-recruit survival rates) as a function of stock-specific parameters at stage one. Then we combine data for multiple stocks by modeling the collection of parameters across multiple stocks at stage two. Finally, we complete the Bayesian model by assigning prior distributions to parameters (hyperparameters) of the second-stage prior distributions.

Pink salmon data

The data we analyze are early summer SSTs and stock–recruitment data of 43 pink salmon stocks with ocean entry points distributed from Puget Sound (Washington, USA) and British Columbia (Canada) to as far north as Norton Sound (northwestern edge of Alaska, USA). The spawner-to-recruit survival rates ($\log_e(R/S)$) of these stocks are calculated from time series of spawner abundance (S) and recruits (R), ranging in duration from 17 to 47 years (brood years 1950–1996), with an average duration of 29 years (Table 1). For a detailed description of the salmon data and sample locations, see Pyper et al. (2001).

As regional measures of ocean temperature, we use SST data collected along the west coast of North America that were compiled by Mueter et al. (2002*b*) from the International Comprehensive Ocean–Atmosphere Data Set (ICOADS, http://www.cdc.noaa.gov/coads/). These are SST anomalies

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Table 1. Summary of data sets for 43 wild pink salmon stocks used in analyses of spawner and recruitment data.

Region	Stock No.	Stock or district	Brood years	*N*	Source[a]
Washington	1	Nooksack[b]	1959–1995	19	1
	2	Skagit[b]	1959–1995	19	1
	3	Stillaguamish[b]	1959–1995	19	1
	4	Snohomish[b]	1959–1995	19	1
	5	Puyallup River[b]	1959–1995	19	1
	6	Hood Canal[b,c]	1959–1995	19	1
	7	Dungeness[b]	1959–1995	19	1
Fraser River	8	Total[b]	1957–1995	20	2, 3
Mainland British Columbia	9	Statistical areas 12, 13, 15, 16[d]	1954–1994	21	4, 5
Central British Columbia	10	Statistical area 10	1950–1995	46	6, 7
	11	Statistical area 9	1950–1996	47	6, 7
	12	Statistical area 8	1950–1996	47	6, 7
Northern British Columbia	13	Statistical area 6	1950–1995	46	6, 7
	14	Statistical area 2E	1950–1995	46	6, 7
Southeast Alaska	15	Southern (districts 101–108)	1960–1996	37	8
	16	Northern inside (109–112, 114, 115)	1960–1996	37	8
	17	Northern outside (113)	1960–1996	37	8
Yakutat	18	Situk River	1962–1990	25	8, 9
	19	Humpy Creek	1962–1992	22	8, 9
Prince William Sound	20	Eastern district	1967–1996	30	10
	21	Montague district	1971–1996	26	10
	22	Southeastern district	1967–1996	30	10
Lower Cook Inlet	23	Southern district[e]	1960–1996	37	11
	24	Outer district[f]	1960–1996	37	11
	25	Kamishak district[g]	1960–1996	34	11
Kodiak Island	26	Afognak district	1980–1996	17	12
	27	Westside district	1980–1996	17	12
	28	Alitak district	1980–1996	17	12
	29	Eastside–Northend district	1980–1996	17	12
	30	Mainland district	1980–1996	17	12
Chignik	31	Chignik Bay district	1962–1995	31	13, 14
	32	Central district	1962–1995	34	13, 14
	33	Eastern district	1962–1995	34	13, 14
	34	Western district	1962–1995	34	13, 14
	35	Perryville district	1962–1995	34	13, 14
Alaska Peninsula	36	Northwestern district	1962–1996	35	13, 15
	37	Southeast district and south-central district	1962–1996	35	13, 16
	38	Southwest district and Unimak district	1962–1996	35	13, 16
Bristol Bay	39	Nushagak district[h]	1960–1996	17	17
Norton Sound	40	Nome	1978–1995	17	18, 19
	41	Golovin	1968–1995	18	18, 19
	42	Moses Point and Norton Bay	1963–1994	24	18, 19
	43	Unalakleet	1962–1995	23	18, 19

Note: Adapted from Pyper et al. (2001). *N* is the number of brood years of data available.

[a]1, Jeff Haymes, Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, WA 98501, USA (personal communication); 2, Al Cass, Canadian Department of Fisheries and Oceans (DFO), Hammond Bay Road, Nanaimo, BC V9R 5K6 (personal communication); 3, Jim Woodey, Pacific Salmon Commission, 600–1155 Robson Street, Vancouver, BC V6E 1B5 (personal communication); 4, Clyde Murray, DFO, Hammond Bay Road, Nanaimo, BC V9R 5K6 (personal communication); 5, Lia Bjesterveld, DFO, 200–401 Burrard Street, Vancouver, BC V6C 3S4 (personal communication); 6, Dennis Rutherford, DFO, Hammond Bay Road, Nanaimo, BC V9R 5K6 (personal communication); 7, Wood et al. (1999); 8, Tim Zadina, Alaska Department of Fish and Game (ADFG), 2030 Sea Level Drive, Ketchikan, AK 99901, USA (personal communication); 9, Clark (1995); 10, Mark Willette, ADFG, 43961 Kalifornsky Beach Road, Suite B, Soldotna, AK 99835, USA (personal communication); 11, Ted Otis, ADFG, 3298 Douglas Place, Homer, AK 99603 USA (personal communication); 12, Kevin Brennan, ADFG, 211 Mission Road, Kodiak, AK 99615, USA (personal communication); 13, Denby Lloyd, ADFG, 211 Mission Road, Kodiak, AK 99615, USA (personal communication); 14, Owen and Sarafin (1999); 15, Murphy et al. (1999); 16, Campbell et al. (1999); 17, Michael Link, ADFG, 333 Raspberry Road, Anchorage, AK 99518, USA (personal communication); 18, Betsy Brennan, ADFG, 333 Raspberry Road, Anchorage, AK 99518, USA (personal communication); 19, Brennan et al. (1998).

[b]Data were only available for odd years (e.g., brood years 1959, 1961,..., 1995) because few if any pink salmon spawn in even years.

[c]Sum of Dosewallips, Duckabush, and Hamma Hamma data sets.

[d]Only even-year data were used for the Mainland British Columbia data set because catches in most odd years were confounded by catch of Fraser River pink salmon.

[e]Sum of Humpy Creek, Port Graham, and Seldovia Bay data sets.

[f]Sum of Port Chatham, Port Dick, Rocky River, and Windy Creek data sets.

[g]Sum of Brown's Peak Creek, Bruin River, and Sunday Creek data sets.

[h]Data were only available for even years because few if any pink salmon spawn in odd years.

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from long-term means at each location (in °C) averaged across those coastal areas occupied by a given pink salmon stock during its early ocean residence period (April–July for stocks in Washington, British Columbia, and Southeast Alaska; May–August for most Alaska stocks; and June–September for stocks in Western Alaska) (Mueter et al. 2002*b*).

We use the SST index defined above because Mueter et al. (2002*b*) found that it has a scale of positive covariation across space similar to that of salmon spawner-to-recruit survival rates. This suggests that summer SST may be an important index of processes driving variation in those survival rates. In a subsequent analysis, summer SST was identified as a significant environmental variable in models of survival rates of Pacific salmon (Mueter et al. 2002*a*).

Modeling the data

Survival rates of M pink salmon stocks ($M = 43$ here) can be described by a standard Ricker model (StdRicker).

$$(1) \qquad y_{it} = \alpha_i - \beta_i S_{it} + \varepsilon_{it}$$

where $y_{it} = \log_e(R_{it}/S_{it})$, which denotes the logarithm of adult recruits produced per spawner (survival rate) for stock i ($i = 1, \ldots, M$) for brood year t (year of spawning); S_{it} is the spawner abundance; R_{it} is the resulting recruitment; the model error term ε_{it} is distributed as $N(0, \sigma_i^2)$; and σ_i^2 is the variance of the error terms.

To examine effects of SST on salmon survival rates, we developed a generalized Ricker model (GRicker) (Quinn and Deriso 1999; Mueter et al. 2002*a*) by including the SST index defined above

$$(2) \qquad y_{it} = \alpha_i - \beta_i S_{it} + \gamma_i \mathrm{SST}_{i,t+1} + \varepsilon_{it}$$

where γ_i is the coefficient of early summer coastal sea surface temperature, $\mathrm{SST}_{i,t+1}$, which is lagged 1 year after spawning to correspond to time of ocean entry of pink salmon stock i. Probabilistic forms of the above equation are

$$(3) \qquad y_{it} | \boldsymbol{\theta}_i \overset{\text{indep}}{\sim} N(\mu_{it}, \sigma_i^2)$$

where μ_{it} denotes the predicted spawner-to-recruit survival rate, with $\mu_{it} = \alpha_i - \beta_i S_{it}$ for the StdRicker model and $\mu_{it} = \alpha_i - \beta_i S_{it} + \gamma_i \mathrm{SST}_{i,t+1}$ for the GRicker model; $\boldsymbol{\theta}_i$ is the parameter vector, with $\boldsymbol{\theta}_i = (\alpha_i, \beta_i, \sigma_i^2)$ for the StdRicker model and $\boldsymbol{\theta}_i = (\alpha_i, \beta_i, \gamma_i, \sigma_i^2)$ for the GRicker model. Equation 3 states that conditional on a set of stock-specific parameters $\boldsymbol{\theta}_i$, the y_{it} are assumed to be independent and normally distributed.

However, salmon stock–recruitment data often show temporal autocorrelation (Adkison et al. 1996), which should be taken into account. To allow for possible dependence among the error terms, we assume in some models that ε_{it} values follow a first-order autoregressive process (AR(1)), $\varepsilon_{it} = \rho_i \varepsilon_{i,t-1} + \xi_{it}$, where $\xi_{it} \sim N(0, \sigma_i^2)$ and ρ_i is the autoregressive coefficient for stock i. In this case

$$(4) \qquad y_{it} = \mu_{it} + \rho_i (y_{i,t-1} - \mu_{i,t-1}) + \xi_{it}$$

for the brood years after the first year. For the first brood year only, we assume that y_{it} was generated by eqs. 1 or 2 without the AR(1) process (Judge et al. 1988). In other models, we also consider the simpler cases where each stock has the same ρ_i value, $\rho_i = \rho$, and the same σ_i^2 value, $\sigma_i^2 = \sigma^2$.

Modeling the parameters

In the next few sections, we develop several alternative hierarchical Bayesian models by specifying a variety of plausible hierarchical prior distributions for α_i and γ_i. Hierarchical priors are conditional probability distributions defined by further unknown parameters (hyperparameters) with their own prior distributions (hyperprior distributions) (Gelman et al. 2004). Hierarchical priors are used to account for potential dependence among parameters across stocks.

We make these alternative prior assumptions based on initial single-stock analyses for which estimates of α_i are similar across pink salmon stocks. Single-stock SST coefficients, however, show a general north–south gradient, with higher values in the north (Mueter et al. 2002*a*). Therefore, in some models we assume a common normal distribution for α_i but more complex priors for the SST coefficients.

We treat other stock-specific parameters (β_i, ρ_i, and σ_i^2) as fixed effects in that their prior distributions are defined with known hyperparameter values. We assign default noninformative prior distributions for these parameters because the data usually contain enough information to estimate these data-level parameters well. We assume noninformative priors for each β_i, $\beta_i \sim N(0, 10^3)$ (i.e., a normal distribution with relatively large variance) and each σ_i^2, $\sigma_i^2 \sim \mathrm{IG}(c, d)$, where $c = d = 0.001$ (a just proper inverse gamma distribution). IG denotes an inverse gamma distribution with shape c, scale d, density $(d^c/\Gamma(c))x^{-(c+1)} \exp(-d/x)$, and mode $d/(c+1)$. We use a uniform prior for $\rho_i \sim U(-1,+1)$ (Chib 1993). In the cases where $\rho_i = \rho$ and $\sigma_i^2 = \sigma^2$ across stocks, we assume $\sigma^2 \sim \mathrm{IG}(0.001, 0.001)$ and $\rho \sim U(-1,+1)$. For the region-specific HBM below, we use ρ_1 and σ_i^2 for southern stocks and ρ_2 and σ_2^2 for northern stocks. The priors assigned for these parameters are $\sigma_i^2 \sim \mathrm{IG}(0.001, 0.001)$ and $\rho_1 \sim U(-1, +1)$, and $\sigma_2^2 \sim \mathrm{IG}(0.001, 0.001)$ and $\rho_2 \sim U(-1,+1)$, respectively.

Spatially correlated prior distribution

To account for the anticipated local similarity of stock-specific parameters, we specify below a spatially correlated prior distribution based on a Gaussian CAR structure (Besag et al. 1991; MacNab and Dean 2000; Banerjee et al. 2004) for γ_i in eq. 2 and (or) α_i in eqs. 1 and 2. The CAR structure specifies the conditional distribution of a parameter given the values of parameters at other locations. In the following, we describe the CAR model using γ_i as an example (the derivation is similar for α_i). The CAR model for γ_i given γ_j, $j \neq i$ (Besag and Higdon 1999), is

$$(5) \qquad \gamma_i | \gamma_j,\ j \neq i \sim N\left(\frac{\sum_{j \neq i} q_{ij} \gamma_j}{\sum_{j \neq i} q_{ij}}, \frac{\tau_\gamma^2}{\sum_{j \neq i} q_{ij}} \right); \quad i, j = 1, \ldots, M$$

where q_{ij} denotes the influence of γ_j values on the conditional expectation of γ_i. Equation 5 has an attractive interpretation: the conditional prior expectation of γ_i is the weighted average of the values of the neighboring γ_j. The τ_γ^2 is a variance parameter controlling the amount of smoothing in γ_i induced by its neighboring values. The joint distribution of the vector $\boldsymbol{\gamma} = (\gamma_1, \ldots, \gamma_M)$ is described in Appendix A.

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The specification of q_{ij} in eq. 5 reflects prior beliefs about the spatial dependence structure among areas, often called neighborhood schemes in spatial statistics (Cressie 1993). The q_{ij} usually take fixed values, implying a fixed and predefined neighborhood scheme. The usual choice is that for areas sharing a common boundary, $q_{ij} = 1$, and $q_{ij} = 0$ otherwise. In that case (an adjacency-based scheme), only the information from a few nearest neighbors on an individual effect is pooled to stabilize its value.

The above scheme is applicable to a study area containing subdivisions with similar size and shape, which is not appropriate for our study, because spatial structure among salmon stocks is essentially represented by their ocean entry points. Thus, the neighborhood consists of pairwise distances between stocks that range continuously along a spectrum from 0 to ~3000 km. Such a structure implies a model for q_{ij} based on interstock distances, d_{ij}, and we propose an exponential decay function

$$(6) \qquad q_{ij} = \exp(-d_{ij}\lambda_\gamma)$$

where q_{ij} are set to zero for all $i = j$ by convention. Here, d_{ij} is the great circle distance between i and j. In this case, the neighborhood scheme varies among stocks and is determined by λ_γ estimated from the data, not by a fixed input from the user. Similar approaches to define q_{ij} by distance measures also exist (E.M. Conlon and L.A. Waller, unpublished data; Banerjee et al. 2004). The relative contribution of the estimated value of γ_j to the conditional expectation of γ_i is reflected by the neighboring weights defined by

$$(7) \qquad \omega_{ij} = \frac{q_{ij}}{\sum_{j \neq i} q_{ij}} = \frac{\exp(-d_{ij}\lambda_\gamma)}{\sum_{j \neq i} \exp(-d_{ij}\lambda_\gamma)}$$

As a result, the individual estimates of γ_i would shrink more towards local levels than towards a global mean value. The parameter λ_γ quantifies the extent of spatial autocorrelation or similarity in γ_i among stocks (Best et al. 1999). Moderately large values of λ_γ put relatively more weight on nearby stocks and less weight on distant stocks, implying spatially structured dependence (clustering), whereas very small (or very large) values of λ_γ imply that the correlation does not vary with distance (close to an exchangeable model).

Spatial hierarchical Bayesian models

We derived several models that made different combinations of assumptions about the similarity among stocks of productivity (α_i) and SST effects (γ_i) (Fig. 1). For these alternative models, we denote the distance-based, CAR prior distribution defined previously for $\boldsymbol{\gamma} = (\gamma_1, \ldots, \gamma_M)$ as $\text{CAR}(\lambda_\gamma, \tau_\gamma^2)$. Similarly, a distance-based, CAR prior distribution for $\boldsymbol{\alpha} = (\alpha_1, \ldots, \alpha_M)$ can be written as $\text{CAR}(\lambda_\alpha, \tau_\alpha^2)$.

Full spatial HBM (CAR–CAR)

First, we develop a full spatial hierarchical Bayesian model in which both the α_i and γ_i parameters of eq. 2 are assumed to have a spatial structure such that parameters for nearby stocks will be more highly correlated than those of more distant stocks. Thus, we assume a CAR prior on both $\boldsymbol{\alpha}$ and $\boldsymbol{\gamma}$: $\boldsymbol{\alpha} \sim \text{CAR}(\lambda_\alpha, \tau_\alpha^2)$, $\boldsymbol{\gamma} \sim \text{CAR}(\lambda_\gamma, \tau_\gamma^2)$, respectively, denoted CAR–CAR here. Such CAR priors can accommodate various spatial patterns in the parameters. An example of the CAR structure for α_i is illustrated in Fig. 1*c*.

The hyperparameters λ_α, λ_γ, τ_α^2, and τ_γ^2 are assumed unknown, and prior distributions must be given for them. We assign λ_α and λ_γ uniform priors in a specified range: $\lambda_\alpha \sim U(0, 2)$ and $\lambda_\gamma \sim U(0, 2)$. The interval $(0, 2)$ was determined by numerical experiment so that it is wide enough to cover the possible values of λ_α and λ_γ.

In Bayesian hierarchical modeling, choosing prior distributions for the hypervariance parameters (e.g., τ_α^2 and τ_γ^2) is particularly difficult but critical. There is often limited information in the data for these parameters. Therefore, their prior distributions can be quite influential. Various noninformative prior distributions have been suggested, including the often-used inverse gamma distribution IG(c, d), with c and d set to 0.001 (Spiegelhalter et al. 1997). Recent discussions in the statistical literature favor the use of a uniform distribution on the hierarchical standard deviation (e.g., $\tau_\alpha \sim U(0, +\infty)$ and $\tau_\gamma \sim U(0, +\infty)$) as a baseline when there is reasonable information from the data (Gelman et al. 2004; Spiegelhalter et al. 2004). But in any case, the default noninformative prior distribution for the data-level error variance $p(\sigma^2) \sim 1/\sigma^2$ is inappropriate for hierarchical variance parameters because it leads to an improper posterior distribution (Gelman et al. 2004).

For the CAR models, weakly informative IG distributions IG(0.01, 0.01) or IG(0.1, 0.1) are often used for the hypervariance parameters to maintain posterior propriety and also to facilitate better mixing of the MCMC chains (Best et al. 1999; Banerjee et al. 2004). Kelsall and Wakefield (1999) suggest an alternative IG(0.5, 0.0005) prior for these parameters. In this paper, we use priors $\tau_\alpha^2 \sim \text{IG}(0.01, 0.01)$ and $\tau_\gamma^2 \sim \text{IG}(0.01, 0.01)$. We also carry out sensitivity analyses to examine the influence of these various prior specifications of τ_α^2 and τ_γ^2 on resulting posterior distributions.

SST spatial only (EXCH–CAR)

Our second type of spatial HBM is identical to the first, except that we assume no spatial structure for α_i in eq. 2 and instead use an exchangeable prior distribution (Fig. 1*b*) for α_i (i.e., $\alpha_i \sim N(\mu_\alpha, \tau_\alpha^2)$), where μ_α is the overall mean and τ_α^2 is the variance. Such prior distributions have the effect of shrinking the distribution of values of individual parameters toward an overall mean value (μ_α). We still assume that $\boldsymbol{\gamma}$ follows the CAR structure: $\boldsymbol{\gamma} \sim \text{CAR}(\lambda_\gamma, \tau_\gamma^2)$, hence this model is denoted EXCH–CAR.

For the two hyperparameters (μ_α and τ_α^2) defining the normal prior distribution of α_i for this exchangeable case, we set a noninformative prior for $\mu_\alpha \sim N(0, 10^3)$, but specify a just proper IG prior for $\tau_\alpha^2 \sim \text{IG}(0.001, 0.001)$ to maintain posterior propriety of the model (Su et al. 2001). The hyperprior distributions of λ_γ and τ_γ^2 are the same as that in the CAR–CAR model.

Other Bayesian models

Region-specific HBM (EXCH–Regional)

In another type of model, we also assign a normal prior for α_i: $\alpha_i \sim N(\mu_\alpha, \tau_\alpha^2)$ as in the EXCH–CAR model, but here we use a region-specific prior for γ_i (hence, called the EXCH–Regional model). This structure is based on the work of Mueter et al. (2002*a*), which showed evidence of different

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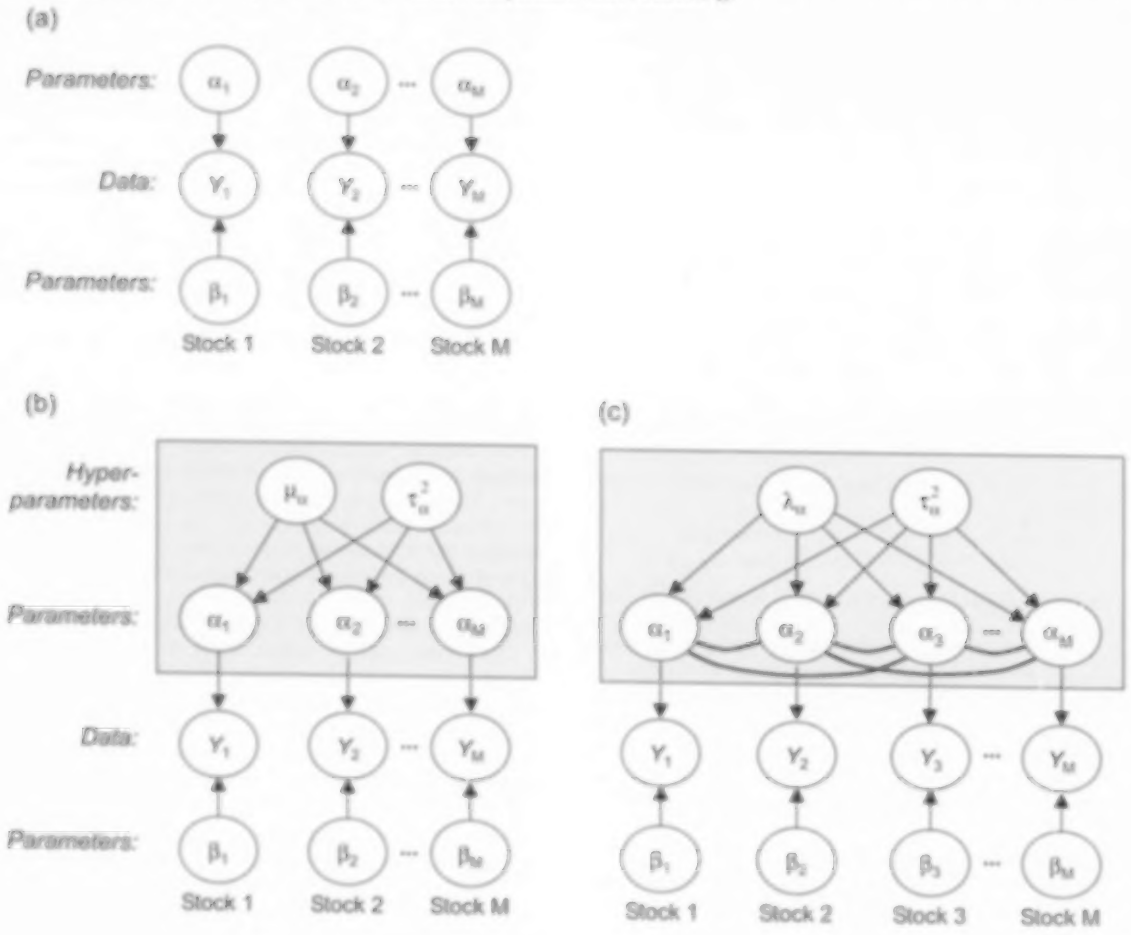
Fig. 1. Schematics of three assumptions about prior distributions for the productivity parameter α_i of the Ricker stock–recruitment model for each of our 43 pink salmon (*Oncorhynchus gorbuscha*) stocks, *i*. A data set for a given stock is represented by the vector Y_i. (*a*) In single-stock analyses, the α_i parameter for a given stock is assumed to be independent of α_j, $j \neq i$, for other stocks; the same applies to β_i. For each stock we assume an independent uniform prior probability distribution, $U(-\infty, +\infty)$, for α_i and another for β_i. (*b*) In a hierarchical Bayesian model with an exchangeable prior distribution for α_i, the α_i parameters are assumed to follow a single common distribution; here a normal distribution with some unknown mean, μ_α, and unknown variance, τ_α^2 (i.e., $N(\mu_\alpha, \tau_\alpha^2)$). The α_i parameter is independent of α_j, $j \neq i$, for other stocks given the two hyperparameters μ_α and τ_α^2 (i.e., α_i and α_j are conditionally independent of each other given the hyperparameters). (*c*) In a spatial hierarchical Bayesian model with a conditional autoregressive (CAR) prior distribution for α_i, the α_i value for any one stock depends on the value for other stocks, in our case, as affected by the distance between stocks (i.e., α_i and α_j are dependent on each other conditionally or unconditionally). This spatial structure is represented by curving lines connecting circles. Assumptions for priors for β_i in (*b*) and (*c*) were the same as in (*a*). In some of our 24 models, we used similar structures for assumptions about sea surface temperature (SST) effects, γ_i.



responses of salmon survival rate to changes in ocean temperature in southern and northern pink salmon. Therefore, we assume one normal prior distribution for γ_i for the southern stocks (Washington and British Columbia, stocks 1–14), $\gamma_{1i} \sim N(\mu_{\gamma 1}, \tau_{\gamma 1}^2)$, and another for the northern stocks (Alaska, stocks 15–43), $\gamma_{2i} \sim N(\mu_{\gamma 2}, \tau_{\gamma 2}^2)$, where $\mu_{\gamma 1}$ and $\mu_{\gamma 2}$ are the overall means and $\tau_{\gamma 1}^2$ and $\tau_{\gamma 2}^2$ are variance terms for southern and northern regions, respectively. The structural scheme for the model of each region's γ_i is analogous to that shown for α_i in Fig. 1*b*. Hyperpriors are assigned to the related hyperparameters analogous to those assigned for μ_α and τ_α^2 in the EXCH–CAR model.

Single-stock Bayesian model

We also derive a single-stock, nonhierarchical model by assigning noninformative priors for all parameters (e.g., $\alpha_i \sim U(-\infty, +\infty)$, $\beta_i \sim U(-\infty, +\infty)$, $\gamma_i \sim U(-\infty, +\infty)$, $\rho_i \sim U(-1, +1)$ and $p(\sigma_i^2) \sim 1/\sigma_i^2$) and by estimating parameters independently for each stock based only on data for that stock (Fig. 1*a*). Thus, no borrowing of information occurs among

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stocks. This is the most commonly used approach in fisheries science.

We form a total of 24 different models for comparison by combining the different data-level model assumptions (i.e., StdRicker or GRicker, with or without AR(1) term, and ρ_i and σ_i^2 being the same (or not) across stocks; see Modeling the data) and the different assumptions for prior probability distributions defined in this section. For the most general, full spatial (CAR–CAR) GRicker HBM with an AR(1) term and different ρ_i and σ_i^2 for each stock, the entire model specification is

(*i*) Stage 1, data level

$$y_{it} = \alpha_i - \beta_i S_{it} + \gamma_i SST_{i,t+1} + \varepsilon_{it}$$

$$\varepsilon_{it} = \rho_i \varepsilon_{i,t-1} + \xi_{it}$$

$$\xi_{it} \sim N(0, \sigma_i^2)$$

(*ii*) Stage 2, prior distributions

$$\boldsymbol{\alpha} \sim \text{CAR}(\lambda_\alpha, \tau_\alpha^2), \quad \boldsymbol{\gamma} \sim \text{CAR}(\lambda_\gamma, \tau_\gamma^2)$$

$$\beta_i \sim N(0, 10^3), \quad \rho_i \sim U(-1, +1), \quad \sigma_i^2 \sim \text{IG}(0.001, 0.001)$$

(*iii*) Stage 3, hyperprior distributions

$$\lambda_\alpha \sim U(0, 2), \quad \lambda_\gamma \sim U(0, 2)$$

$$\tau_\alpha^2 \sim \text{IG}(0.01, 0.01), \quad \tau_\gamma^2 \sim \text{IG}(0.01, 0.01)$$

Bayesian estimation and model comparison by MCMC methods

Based on the previous model specifications, the joint posterior probability distribution of all parameters for the full spatial model (CAR–CAR) is

$$(8) \quad p(\lambda_\alpha)p(\lambda_\gamma)p(\tau_\alpha^2)p(\tau_\gamma^2)\text{CAR}(\boldsymbol{\alpha}|\lambda_\alpha, \tau_\alpha^2)\text{CAR}(\boldsymbol{\gamma}|\lambda_\gamma, \tau_\gamma^2)\prod_{i=1}^{M} p(\beta_i)p(\rho_i)p(\sigma_i^2)\prod_{i=1}^{M}\prod_{t=1}^{n_i} p(y_{it}|\boldsymbol{\theta}_i)$$

$$\propto U(\lambda_\alpha|0, 2)U(\lambda_\gamma|0, 2)\,\text{IG}(\tau_\alpha^2|0.01, 0.01)\text{IG}(\tau_\gamma^2|0.01, 0.01)\,\text{CAR}(\boldsymbol{\alpha}|\lambda_\alpha, \tau_\alpha^2)\text{CAR}(\boldsymbol{\gamma}|\lambda_\gamma, \tau_\gamma^2)$$

$$\times \prod_{i=1}^{M} N(\beta_i|0, 10^3)U(\rho_i|-1, +1)\text{IG}(\sigma_i^2|0.001, 0.001)\prod_{i=1}^{M}\prod_{t=1}^{n_i} N(y_{it}|\mu_{it} + \rho_i(y_{i,t-1} - \mu_{i,t-1}), \sigma_i^2)$$

where $\boldsymbol{\theta}_i = (\alpha_i, \beta_i, \gamma_i, \rho_i, \sigma_i^2)$. Posteriors for other models can be derived similarly. We estimate model parameters by simulating from the posterior distributions of the models via a hybrid Metropolis–Gibbs sampler (see Su et al. 2001), which is an MCMC method (Gilks et al. 1996). For this method, we require the full conditional posterior distribution of each parameter (or set of parameters), given the remaining parameters (Su et al. 2001).

Full conditional distributions can be derived from the joint posterior distribution (e.g., eq. 8; Su et al. 2001). For the CAR–CAR model, the conditional distributions of α_i, β_i, and γ_i are normal distributions, that of ρ_i is a truncated normal distribution, and those of σ_i^2, τ_α^2, and τ_γ^2 are IG distributions. Therefore, we use Gibbs steps to update these parameters by generating samples from normal and IG distributions. However, the full conditionals of λ_α and λ_γ are not standard distributions because they appear nonlinearly in the precision matrix $\mathbf{H}_\alpha$ or $\mathbf{H}_\gamma$ (Appendix A). We update these two parameters using univariate Metropolis steps (Su et al. 2001).

We implemented all of the models in a Borland Delphi (Borland Software Corporation, Scotts Valley, California) program. We also used the WinBUGS software to perform the estimation (Spiegelhalter et al. 1997). The two programs yielded almost identical results, but our program runs faster. All of these Bayesian models were compared by the DIC proposed by Spiegelhalter et al. (2002) (Appendix B).

Convergence diagnostics

We adopted a multiple chain approach for posterior simulation (Gelman et al. 2004). In the following, we ran five chains with dispersed starting values of parameters for each proposed model. For the HBMs with one or two spatial components ($\boldsymbol{\alpha}$ or $\boldsymbol{\gamma}$), we first ran the hybrid Metropolis–Gibbs sampler for an initial period of 3000 iterations for each chain. This procedure tuned the standard deviations of the normal proposal distributions used in the Metropolis steps for updating the values of λ_α (for CAR–CAR) and λ_γ (for both kinds of models) to obtain an acceptance rate between 20% and 40% (Su et al. 2001). These initial iterations were subsequently ignored. This tuning step was not needed for other models where all the full conditionals are standard distributions. After the tuning period, we ran the sampler for many additional iterations for each model to assess the convergence of the chains.

We conducted extensive diagnostic tests, including monitoring the values of Gelman–Rubin's scale reduction factor (Gelman et al. 2004), examining autocorrelations of each parameter within a chain and cross correlations among parameters and other convergence diagnostics (Best et al. 1995). These diagnostics indicated that the chains of hyperparameters, especially those in the CAR priors, usually showed slow mixing. For example, the effective sample size (Gelman et al. 2004) of τ_γ^2 is only one quarter of that of stock-specific parameters in an EXCH–CAR model, reflecting high autocorrelation of this parameter. However, based on the scale reduction factor and other diagnostics, all models showed no evidence of not converging (Gill 2002) after a burn-in period of 2000 iterations. We ran the Gibbs sampler for each model for 50 000 iterations for each chain with a thinning interval of 10 iterations. We discarded the first 2000 iterations as burn-in and used the rest of the chains to calculate posterior means and 95% probability inter-

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Table 2. Model-checking quantities for alternative models with the standard Ricker formula (StdRicker, eq. 1) as the data-level structure.

	Quantity						
Model	ρ	σ^2	Np	No.	p_D	$\bar{D}$	DIC
Single-stock	NA	Same	87	1	87	3486	3573
	NA	Diff	129	2	133	3374	3507
	Same	Same	88	3	88	3479	3567
	Diff	Diff	172	4	177	3357	3534
EXCH	NA	Same	87	5	75	3485	3560
	NA	Diff	129	6	116	3375	3491[a]
	Same	Same	88	7	75	3478	3552
	Diff	Diff	172	8	158	3358	3516

Note: ρ, autocorrelation in residuals; σ^2, variance of residuals; NA, not applicable; Same, same value for all stocks; Diff, different values for each stock; No., the model number referred to in the text; Np, the nominal number of parameters in a model; p_D, the effective number of parameters; $\bar{D}$, the posterior average of deviance. Single-stock models 1–4 assume that α_i and β_i for all stocks are independent. Multistock hierarchical EXCH models 5–8 assume that α_i values are drawn from a single, normal distribution (i.e., no spatial structure).

[a]The case with the best fit or lowest deviance information criterion (DIC) of the eight models.

vals for all parameters of the models. We also calculated the deviance $D(\theta^{(k)})$ (Appendix B, eq. B1) during the sampling process.

Results

Comparison of models

We compared our models in terms of DIC and the effective number of parameters (p_D) (Tables 2 and 3; Fig. 2). These values are subject to minor simulation error; we therefore calculated DIC for different starting values of the parameters and different random number seeds. This resulted in differences in DIC for each model of no more than ±1 DIC unit, so that differences in DIC of more than about 4 indicate that differences in model fit are not likely to be attributable to sampling error.

Many results emerged from comparing our 24 models. First, models that incorporated the effect of SST (GRicker models 9–24) gave a much better fit to the data (i.e., had lower DIC) for all pink salmon stocks than models that omitted the SST effect (StdRicker models 1–8) (Fig. 2). For instance, the best StdRicker model (6) was a multistock HBM, with α_i values assumed to be drawn independently from the same distribution (i.e., exchangeable, EXCH), no AR(1) term for the residual errors, and different σ^2 for these residuals for each stock (Table 2). The DIC for that model (3491) was considerably lower than that of the other seven StdRicker models, but is much larger than DIC values for GRicker models that incorporated SST (Fig. 2, compare models 1–8 with models 9–24).

Second, multistock HBMs performed better than their single-stock counterparts in all cases (Tables 2 and 3). For instance, in each pair of analogous models (1 and 5, 2 and 6, etc., in Table 2, as well as 9 and 13, 9 and 17, 9 and 21, etc., in Table 3), the HBMs (the second model in each pair) had a lower DIC than the comparable single-stock model.

Third, models that assumed that each pink salmon stock can have a different σ^2 for their residual errors in eqs. 1 or 2 had better fits to the data than comparable models that assumed the same σ^2 across stocks (e.g., compare models 2 and 1, models 4 and 3, etc., in Table 2 and models 14 and 13, models 18 and 17, etc., in Table 3).

Fourth, among all types of models that assumed residual σ^2 to be stock-specific (denoted as Diff in Tables 2 and 3), models that omitted an AR(1) term (indicated by NA under ρ) fit better than models using a stock-specific ρ(Diff) in the AR(1) term (e.g., model 14 fit better than 16, 18 fit better than 20).

The best models were two spatial HBMs (14 and 18). These models did not have an AR(1) term but allowed for different σ^2 among stocks. Their DIC values are very close, and both are significantly smaller than those of other models (Table 3). The EXCH–CAR model 14 has a very similar model fit ($\bar{D}$) and complexity, or effective number of parameters (p_D), as the full spatial (CAR–CAR) model 18, suggesting that the CAR prior for γ_i, combined with stock-specific σ^2 and the lack of an AR(1) term, have brought improvement in model fit for these spatial models. The prior assumptions for α_i had little effect on model fit (Table 3 and Fig. 2). The fit ($\bar{D}$) of regional model 22 is worse than the two spatial models, but its p_D is smaller (i.e., the model is less complex) than those of the other models, so it has a DIC very close to the two spatial models.

It is instructive to compare the actual number of parameters, Np, with the effective number of parameters, p_D. The values of Np for single-stock, nonhierarchical models were either equal to or very close to p_D, suggesting that no borrowing of information occurred for these models (Table 2, models 1–4, and Table 3, models 9–12). For instance, for single-stock model 9, there were three stock-specific parameters for each of the 43 stocks plus a single common σ^2 for residuals, so Np was 130; p_D also turned out to be 130. In contrast, p_D values for the HBMs were much less than the corresponding Np (Table 2, models 5–8, and Table 3, models 13–24), especially for the GRicker model that included the effect of sea surface temperature. Apparently there was substantial borrowing of information for these HBMs.

In the following, we only discuss the GRicker models without an AR(1) term for residuals but with stock-specific σ_i^2 (models 10, 14, 18, and 22). These models had better fits

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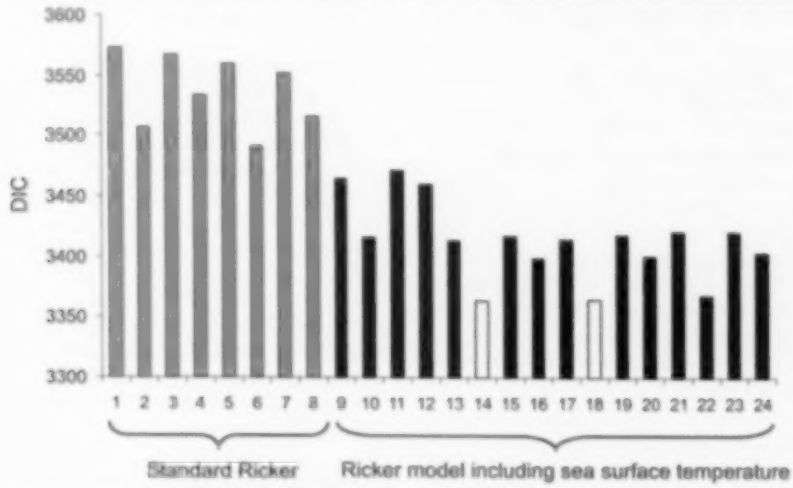
Table 3. Model-checking quantities for the models with sea surface temperature (SST) as an explanatory variable (Generalized Ricker model (GRicker), eq. 2).

	Quantity						
Model	ρ	σ^2	Np	No.	p_D	$\bar{D}$	DIC
Single-stock	NA	Same	130	9	130	3334	3465
	NA	Diff	172	10	179	3237	3416
	Same	Same	131	11	131	3340	3471
	Diff	Diff	215	12	220	3241	3461
EXCH–CAR	NA	Same	130	13	89	3325	3414
	NA	Diff	172	14	134	3230	3364[a]
	Same	Same	131	15	88	3330	3417
	Diff	Diff	215	16	170	3228	3399
CAR–CAR	NA	Same	130	17	88	3326	3414
	NA	Diff	172	18	134	3230	3364[a]
	Same	Same	131	19	88	3331	3419
	Diff	Diff	215	20	170	3230	3400
EXCH–regional	NA	Same	130	21	88	3333	3421
	NA	Diff	172	22	133	3235	3368
	Same	Same	131	23	86	3335	3421
	Diff	Diff	215	24	169	3234	3404

Note: Models 9–12 are single-stock cases, whereas models 13–24 are multistock, hierarchical models. Symbols are as in Table 2. Additionally, CAR indicates the conditional autoregressive prior distribution. CAR–CAR indicates that both α_i and γ_i have spatial structure described by CAR prior distributions. EXCH–CAR is similar to CAR–CAR, except that α_i is assumed to have no spatial structure. EXCH–regional assumes that α_i has no spatial structure but that γ_i has a different prior distribution for northern and southern stocks.

[a]The cases with the best fit or lowest deviance information criterion (DIC) of the 16 models (9–24).

Fig. 2. Comparison of the performance of alternative models using the deviance information criterion (DIC) for 43 stocks of Northeast Pacific pink salmon (*Oncorhynchus gorbuscha*). Model numbers on the *x* axis are defined in Tables 2 and 3. The best-fitting models (14 and 18, open bars) have nearly identical DIC values. Shaded bars are for models that did not include sea surface temperature.



than models with other assumptions for AR(1) and σ_i^2 (Table 3).

HBMs versus single-stock approach

Posterior inference for the coefficients of SST, γ_i

Posterior probability distributions for the coefficients of SST, γ_i, obtained from spatial HBM and single-stock approaches illustrate the advantages of multistock HBMs. The estimates of SST effects from the single-stock approach exhibit large uncertainty (Fig. 3). For example, there are nine stocks with values of coefficients of variation (CV) exceeding 40%, and the average CV value for all stocks is 26%. The 95% probability intervals of about three-quarters of the stocks include the value of zero, meaning no significant effect of SST on survival rates for these stocks. Owing to these large variances in individual SST effects, spatial HBM 18, which allows for similarity among γ_i for nearby stocks, brings substantial shrinkage of point estimates of SST effects toward their local means for most stocks (e.g., the av-

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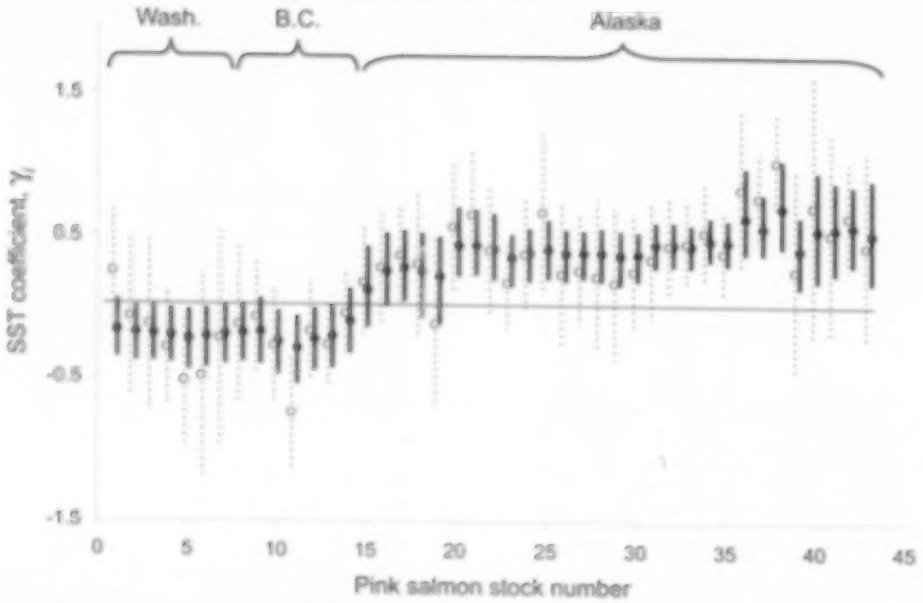
Fig. 3. Posterior inferences (median and 95% probability intervals) for sea surface temperature (SST) effects, γ_i, obtained from the multistock spatial hierarchical Bayesian model (HBM) 18 (solid circles and vertical solid lines) and the comparable single-stock approach (model 10, open circles and vertical dotted lines). Medians were very close to mean values for all stocks. The parameter γ_i expresses the change in $\log_e$(recruits per spawner) per degree Celsius increase in SST (eq. 2). Stock numbers 1–7 are for Washington, 8–14 are for British Columbia, and the rest are for Alaska (defined in Table 1).



erage shrinkage is 51%) (Fig. 3). Thus, the estimates of SST effects of nearby stocks are more similar and consistent and are less variable among stocks than those obtained from the single-stock approach. Furthermore, the average CV of estimates of γ_i from the spatial HBM 18 is only 4.8%.

The multistock approach also substantially reduced the uncertainty of SST effects compared with the single-stock approach (Fig. 3). The average length of the 95% probability intervals obtained from multistock spatial HBM 18 is less than one-half (0.48) of that obtained from single-stock analyses, and about three-quarters of the stocks have SST effects significantly different from zero. Thus, the multistock approach more clearly shows the spatial pattern of SST effects across stocks than the single-stock approach. Specifically, SST has opposite signs of effects on survival rates ($\log_e(R/S)$) in northern and southern stocks.

Posterior inference for the productivities, α_i

The best multistock spatial HBM 18 showed considerable variation among the 43 pink salmon stocks in their mean productivities α_i (Table 4). However, unlike the estimates of γ_i for model 18, there is considerably less shrinkage in point estimates (e.g., the average percent shrinkage is 9%) and less reduction in 95% probability intervals for α_i (Fig. 4) compared with estimates for the single-stock approach. The average length of the 95% probability intervals obtained from the multistock spatial HBM is 0.84 of that obtained from the single-stock analysis. Exceptions in which those intervals were considerably narrower were stocks 2, 8, 20, 26, 39, and 43 (Fig. 4). Median estimates of α_i of the multistock spatial HBMs for stocks 1, 6, 20, 21, 26, 27, 31, 40, 41, and 43 also showed large shrinkage toward their overall mean value.

Spatial versus regional HBMs

To show the benefits of spatial HBMs as compared with regional HBMs, we superimposed the posterior median estimates of SST effects from the best full spatial HBM (model 18) on the median estimates from the regional HBM (model 22) (Fig. 5). The latter model can be thought of as a Bayesian version of the ME model of Mueter et al. (2002*a*).

The influences of different assumptions of models and hierarchical prior distributions are apparent. The estimates of SST effects from the regional HBM are pulled toward their respective mean values in the southern and northern areas, whereas estimates of the spatial HBM model are more similar to those of their neighboring stocks. The difference in results between the two models is most apparent in southeastern Alaska (stocks 15–19, Fig. 5).

Sensitivity analyses of prior specifications

We observed considerable sensitivity to prior assumptions concerning τ_γ^2 and λ_γ under the CAR spatial models. For example, a prior of IG(0.5, 0.0005) on τ_γ^2, which has a mode of 0.0003 and favors variance values less than 0.015, yields a posterior median value of 0.0008 in models 14 and 18 (Table 5). This median value is much smaller than 0.0124 and 0.0121 obtained from a prior of IG(0.01, 0.01) on τ_γ^2, which has a mode of 0.0099. As well, the medians of λ_γ were about doubled under the prior of IG(0.5, 0.0005) for τ_γ^2 compared with using IG(0.01, 0.01) (Table 5). Much less sensitivity is observed for τ_α^2 and λ_α (Table 5). The relatively high sensi-

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Table 4. Posterior summary for α_i from the full spatial model 18.

α_i	Mean	SD	2.5%	97.5%
α_1	1.717	0.250	1.211	2.193
α_2	1.456	0.280	0.901	2.003
α_3	1.190	0.272	0.654	1.721
α_4	1.319	0.275	0.775	1.865
α_5	1.385	0.304	0.786	1.984
α_6	0.895	0.291	0.326	1.473
α_7	1.009	0.271	0.478	1.540
α_8	1.427	0.201	1.027	1.820
α_9	1.433	0.233	0.971	1.891
α_{10}	1.686	0.223	1.247	2.126
α_{11}	1.622	0.213	1.201	2.039
α_{12}	1.063	0.182	0.707	1.421
α_{13}	1.234	0.199	0.838	1.625
α_{14}	0.409	0.180	0.058	0.763
α_{15}	1.363	0.164	1.040	1.685
α_{16}	1.159	0.186	0.793	1.526
α_{17}	0.542	0.168	0.216	0.876
α_{18}	1.365	0.292	0.785	1.935
α_{19}	1.315	0.272	0.775	1.849
α_{20}	1.584	0.345	0.906	2.258
α_{21}	0.692	0.261	0.188	1.215
α_{22}	1.138	0.267	0.615	1.665
α_{23}	0.989	0.234	0.533	1.452
α_{24}	0.980	0.246	0.496	1.464
α_{25}	0.984	0.231	0.532	1.436
α_{26}	1.603	0.325	0.961	2.240
α_{27}	1.763	0.244	1.263	2.224
α_{28}	1.309	0.215	0.882	1.734
α_{29}	1.033	0.272	0.503	1.576
α_{30}	0.901	0.177	0.559	1.260
α_{31}	2.374	0.273	1.804	2.878
α_{32}	0.976	0.210	0.569	1.393
α_{33}	0.870	0.181	0.516	1.232
α_{34}	1.733	0.220	1.298	2.162
α_{35}	1.240	0.203	0.841	1.639
α_{36}	0.941	0.228	0.496	1.391
α_{37}	1.486	0.223	1.042	1.915
α_{38}	1.359	0.230	0.899	1.807
α_{39}	1.227	0.308	0.615	1.833
α_{40}	0.476	0.374	−0.252	1.218
α_{41}	0.419	0.368	−0.294	1.154
α_{42}	0.384	0.236	−0.070	0.856
α_{43}	1.375	0.327	0.723	2.010

Note: i, stock number; SD, standard deviation. Median values were very close to means for all stocks.

tivity of τ_γ^2 and λ_γ may be caused by confounding between these parameters (Best et al. 1999) and lack of information in the data about their values, as indicated by the large uncertainty in single-stock estimates of SST effects, γ_i. On the other hand, estimates of μ_α and τ_α^2 for model 14 are very robust to different prior assumptions (Table 5).

Nevertheless, stock-specific parameter estimates are much less affected by these prior assumptions. For example, coefficients of effects of SST, γ_i, retain a similar spatial pattern across stocks under different priors of τ_γ^2; that pattern also differs from the one obtained from the single-stock approach (Fig. 6).

Discussion

We developed hierarchical Bayesian models that explicitly incorporate spatial correlations among multiple salmon stocks in their productivities and effects of SST. We applied these distance-based spatial HBMs to analyze environmental and stock–recruitment data of pink salmon stocks. Our first major finding is that incorporating early summer coastal SST effects into models significantly improved their fit to the data. Also, spatial HBMs produced more consistent and precise estimates of SST effects than the single-stock approach. As in Mueter et al. (2002*a*), we found significant positive effects of SST on spawner-to-recruit survival rates of northern pink salmon stocks (increased survival rates as SST increased) and weaker negative effects of SST on survival rates of southern pink salmon stocks.

The spatial HBM is a direct extension of and improvement upon Mueter et al.'s (2002*a*) ME model. They used "iid" normal population distributions to model association or similarity among stocks. However, the SST coefficients across stocks show a general north–south gradient, with higher values in the north, which cannot be modeled by a common population distribution. To use the normal population distribution for the random effects, Mueter et al. (2002*a*) assumed a different mean for the southern and northern regions and set a break point between them. They then fit the data for the two regions separately. Estimating two regional means precludes the possibility that there is a smooth transition in effects of SST between the two regions. By relaxing Mueter et al.'s (2002*a*) "iid" normal assumption that assumed a separate mean SST effect in the north and south, we obtain more sensible estimates (not a step function) of SST effects for this transition area (northern British Columbia and southeast Alaska) and avoid possible overshrinkage effects for the SST coefficients.

A general concern is sometimes raised about spawner and recruit data such as ours that cover stocks from various regions: a variety of ways of estimating spawner abundance in the regions may lead to different biases in those estimates. However, such concerns are not relevant to our interpretation above of the geographical changes in estimated effects of SST on $\log_e$(recruits per spawner). This becomes apparent by inspecting eq. 2 and recalling that $y_{it} = \log_e(R_{it}/S_{it})$. That equation shows that a consistent bias in estimates of S_i will change the average level of y_{it} independent of the level of SST. That bias will thus be attributed to the intercept α_i rather than to the effect of SST, γ_i. Care must therefore be taken when interpreting trends in estimates of α_i across large geographical regions (in any case, no such trend appears in our results).

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Fig. 4. Posterior inferences (median and 95% probability intervals) for the productivity parameter of the Ricker model, α_i, obtained from the multistock spatial hierarchical Bayesian model (HBM) 18 (solid circles and vertical solid lines) and the single-stock approach (model 10, open circles and vertical dotted lines). Stock numbers 1–7 are for Washington, 8–14 are for British Columbia, and the rest are for Alaska (defined in Table 1).

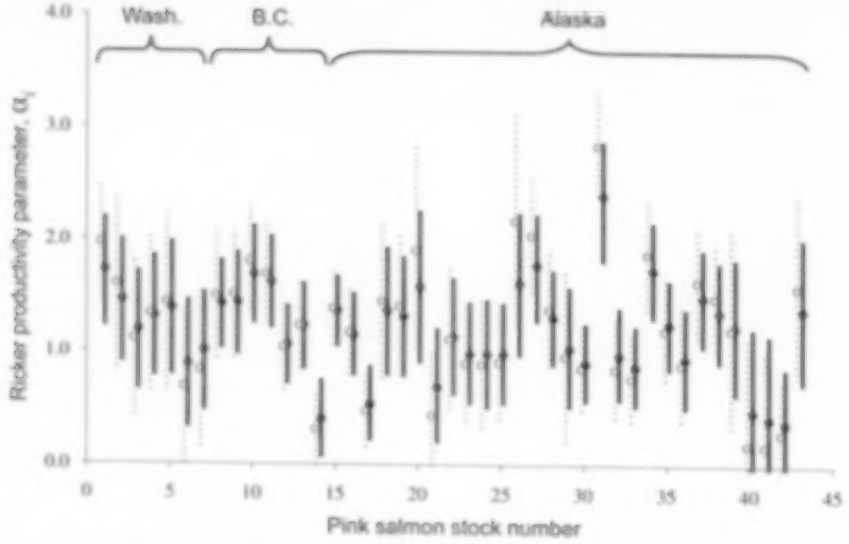
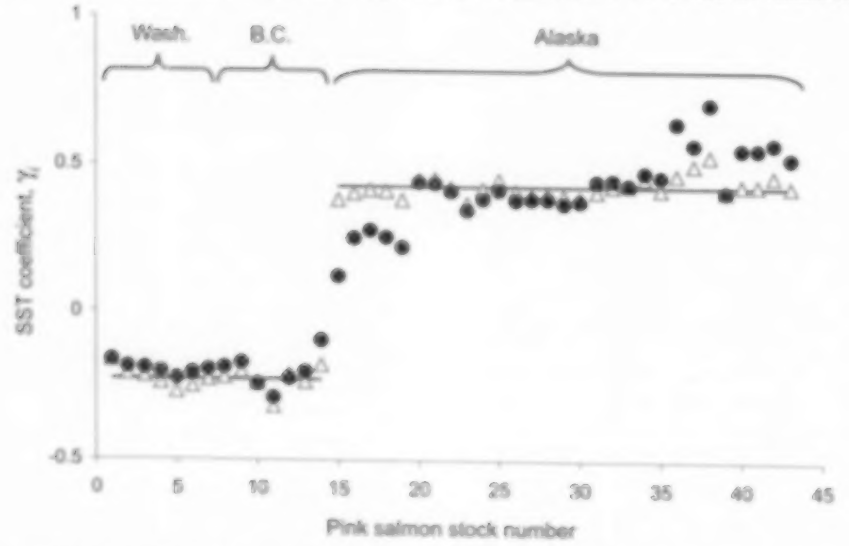


Fig. 5. Posterior medians of the sea surface temperature (SST) effects, γ_i, from the full spatial hierarchical Bayesian model (HBM) 18 (solid circles) and the regional model 22 (open triangles). Horizontal lines show overall mean values of γ_i in southern and northern areas from model 22. Stock numbers 1–7 are for Washington, 8–14 are for British Columbia, and the rest are for Alaska (defined in Table 1).



Our findings suggest that early summer coastal SST might be a useful additional explanatory variable in models of survival rates ($\log_e(R/S)$) for most pink salmon stocks. Nevertheless, the linear predictor that includes SST only explains a small portion of the total variation in survival rates for individual stocks; therefore, improvement in recruitment forecasts by including SST might not be large. However, improvement in estimates for Ricker stock-specific parameters α_i can be helpful for setting reference points for salmon management, with the above-noted caution.

Our results and conclusions about the benefits of spatial hierarchical Bayesian models concur with research in other fields. For example, CAR priors are used extensively in mapping applications of epidemiology (Besag et al. 1991; Waller et al. 1997), where studies of geographical patterns of disease are very important for generating and refining hypotheses as well as for assessment of environmental justice (Waller et al. 1997). Empirical or hierarchical Bayesian models have proven useful in smoothing crude maps of disease risk based on the usual Bayesian borrowing of strength

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Table 5. Summary of the posterior probability distributions of hyperparameters for spatial models 14 and 18 under different prior distributions for τ_α^2 and τ_γ^2.

(*a*) Model 14: EXCH–CAR.

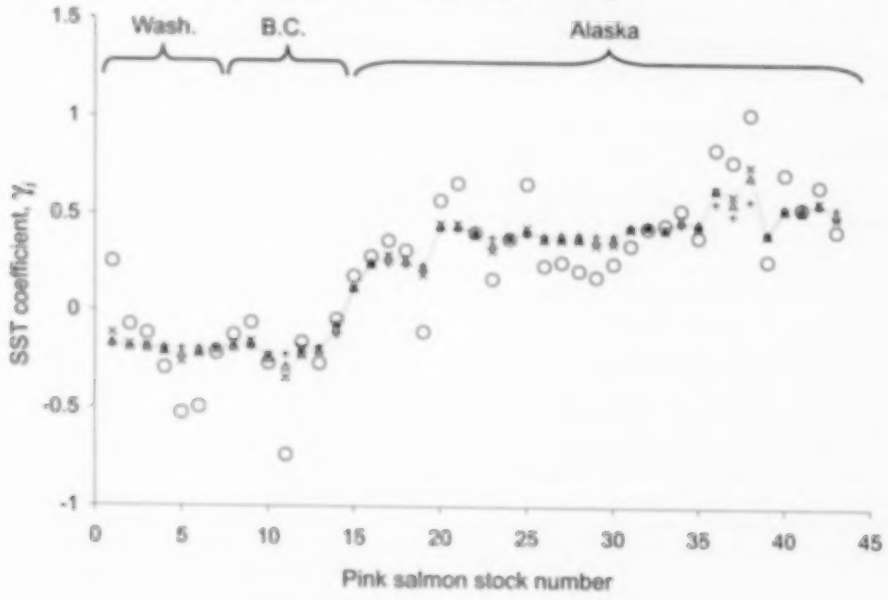
Priors for τ_α^2 (or τ_α) and τ_γ^2	Parameter[a]	μ_α	τ_α^2	τ_γ^2	λ_γ
$\tau_\alpha \sim U(0, +\infty)$ and $\tau_\gamma^2 \sim$ IG(0.1, 0.1)	Median	1.204	0.242	0.0600	0.0049
	Interval	(1.032, 1.382)	(0.134, 0.436)	(0.0193, 0.2537)	(0.0021, 0.0104)
$\tau_\alpha \sim U(0, +\infty)$ and $\tau_\gamma^2 \sim$ IG(0.01, 0.01)	Median	1.203	0.240	0.0124	0.0086
	Interval	(1.029, 1.376)	(0.134, 0.429)	(0.0027, 0.0970)	(0.0031, 0.0173)
$\tau_\alpha \sim U(0, +\infty)$ and $\tau_\gamma^2 \sim$ IG(0.001, 0.001)	Median	1.199	0.234	0.0024	0.0123
	Interval	(1.030, 1.373)	(0.134, 0.430)	(0.0004, 0.0443)	(0.0041, 0.0242)
$\tau_\alpha \sim U(0, +\infty)$ and $\tau_\gamma^2 \sim$ IG(0.5, 0.0005)	Median	1.200	0.240	0.0008	0.0148
	Interval	(1.023, 1.375)	(0.133, 0.432)	(0.0001, 0.0147)	(0.0053, 0.0278)
$\tau_\alpha^2 \sim$ IG(0.001, 0.001) and $\tau_\gamma^2 \sim$ IG(0.5, 0.0005)	Median	1.200	0.231	0.0008	0.0149
	Interval	(1.027, 1.373)	(0.127, 0.414)	(0.0001, 0.0122)	(0.0054, 0.0280)

(*b*) Model 18: CAR–CAR.

Priors for τ_α^2 and τ_γ^2	Parameter[a]	τ_α^2	λ_α	τ_γ^2	λ_γ
IG(0.1, 0.1)	Median	1.839	0.0022	0.0598	0.0049
	Interval	(0.402, 9.752)	(0.0001, 0.0076)	(0.0191, 0.2433)	(0.0022, 0.0105)
IG(0.01, 0.01)	Median	1.733	0.0023	0.0121	0.0087
	Interval	(0.381, 9.327)	(0.0001, 0.0080)	(0.0027, 0.0900)	(0.0031, 0.0173)
IG(0.5, 0.0005)	Median	1.338	0.0029	0.0008	0.0147
	Interval	(0.279, 8.209)	(0.0002, 0.0093)	(0.0001, 0.0135)	(0.0052, 0.0283)

[a]Values for each parameter are shown at the median and extremes of the 95% probability intervals.

Fig. 6. Posterior median values for sea surface temperature (SST) effects, γ_i, obtained from the single-stock approach (model 10, open circles) and the comparable multistock spatial model 14, the latter using different prior probability distributions for τ_α^2 (or τ_α) and τ_γ^2 (connected by lines: +, IG(0.5, 0.0005); △, IG(0.01, 0.01); ×, IG(0.1, 0.1)). Quite similar, stock-specific estimates for γ_i for the multistock spatial model resulted from assuming these three different prior probability distributions. Stock numbers 1–7 are for Washington, 8–14 are for British Columbia, and the rest are for Alaska (defined in Table 1).



property, eliminating the instability of separate maximum likelihood estimates for rare diseases and (or) for low-population areas while maintaining geographic resolution.

The spatial hierarchical Bayesian models used in this paper contain many structural and functional assumptions at different levels of the hierarchy. We dealt with some of these

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assumptions, for example, the data-level error assumptions, by using different priors for stock-specific parameters. Even with this limited set of assumptions, we obtained 24 different model forms. We also conducted sensitivity analyses to examine the influence of prior specifications of τ_γ^2 and τ_α^2 on posterior inference (e.g., changing the values of c and d in IG(c, d)). Although hyperparameters, especially τ_γ^2 and λ_γ, are sensitive to the prior assumptions of τ_γ^2, the estimates of stock-specific parameters (α_i, β_i, and γ_i) were much less sensitive to changes in those prior specifications.

Although we modeled the spatial dependence (i.e., similarity of parameter values in nearby areas) of α_i on α_j, $j \neq i$ (or γ_i on γ_j, $j \neq i$), by using Gaussian CAR specifications (Besag et al. 1991), there are other methods. An alternative approach for modeling spatial autocorrelation is directly formulating the covariance matrix Σ of a multivariate normal distribution of the random effects (e.g., $\gamma \sim \text{MVN}(\mu, \Sigma)$) (Banerjee et al. 2004). But this latter approach is computationally intensive because of a matrix inversion step required for each iteration of the MCMC sampler. In contrast, our conditional approach is computationally very efficient because of the conditional structure of eq. 5 (Banerjee et al. 2004). One disadvantage of the CAR model is that the precision matrix is often singular, making the covariance matrix undefined (Banerjee et al. 2004).

For the distance-based CAR model, different weighting functions other than an exponential decay (eq. 6) are worth considering in the future. Other possible model extensions include using multivariate CAR priors to model potential cross-correlation between the α_i and γ_i parameters of each stock, for instance.

In conclusion, hierarchical Bayesian models that allow for spatial structure of parameter values among multiple salmon stocks may help to more precisely estimate parameters of stock–recruitment models. The resulting models should provide an improved basis for setting conservation and management goals and regulations.

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Appendix A. Joint conditional autoregressive (CAR) distribution.

The joint distribution of vector $\gamma = (\gamma_1, \ldots, \gamma_M)$ can be derived from eq. 5 as follows (Besag and Higdon 1999):

$$(A1) \quad p(\gamma|\tau_\gamma^2, \lambda_\gamma) \propto (\tau_\gamma^2)^{M/2} |\mathbf{H}_\gamma|^{1/2} \exp\left(-\frac{1}{2\tau_\gamma^2}\gamma' \mathbf{H}_\gamma \gamma\right)$$

where $\mathbf{H}_\gamma$ is a matrix with elements H_{ij} given by $H_{ij} = -q_{ij}$ for $j \neq i$ and $H_{ij} = \Sigma_{j \neq i} q_{ij}$ for $j = i$. Matrix $\mathbf{H}_\gamma$ is not full rank (its row and column sums are zero), indicating that the CAR prior (eq. A1) is improper. Here, $|\mathbf{H}_\gamma|$ denotes the product of only the non-zero eigenvalues of $\mathbf{H}_\gamma$ (Besag and Higdon 1999).

The CAR prior (eq. A1) is a special case of the pairwise difference priors (Besag et al. 1995), which are all improper. They specify only differences in γ_i, not their overall level, and so are identified only up to an additive constant (adding an arbitrary constant to each γ_i does not change the probability). To permit the data to identify the overall level, we need (1) to constrain the γ_i values to sum to zero, (2) to set one of γ_i to a fixed value, or (3) to omit the overall level. In

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our model, an overall level is not specified for either α_i or γ_i (eq. 2) (i.e., we use option 3).

Appendix B. Deviance information criterion (DIC).

To compare the fit of different models to the data, we calculate the DIC (Spiegelhalter et al. 2002). Let the deviance $D(\boldsymbol{\theta})$ be minus twice the log-likelihood of the data and $\boldsymbol{\theta}$ be the parameter vector. Then

$$\text{DIC} = \text{"fit"} + \text{"complexity"}$$

where fit is defined as the posterior expectation of the deviance $D(\boldsymbol{\theta})$, $\bar{D} = E_{\boldsymbol{\theta}|y}(D)$, and complexity is represented by the effective number of parameters p_D, which is defined as $p_D = \bar{D} - D(\bar{\boldsymbol{\theta}})$, where $D(\bar{\boldsymbol{\theta}})$ is the deviance evaluated at the posterior expectations of $\boldsymbol{\theta}$, $\bar{\boldsymbol{\theta}}$. Typically, the effective number of parameters p_D will be less than the total actual number of parameters in a hierarchical Bayesian model, owing to the borrowing of strength across random effects. A smaller value of DIC indicates a better-fitting model.

Note that DIC is not intended for identification of the correct model, but rather is a method of comparing a collection of alternative models (all of which may be incorrect). DIC is scale-free. Thus, the values of DIC have no intrinsic meaning; only differences in DIC across models are meaningful (Banerjee et al. 2004).

An attractive feature of DIC is that it may be readily calculated during an MCMC run by monitoring both $\boldsymbol{\theta}$ and $D(\boldsymbol{\theta})$; at the end of the run, simply take the mean of the simulated values of $D(\boldsymbol{\theta})$ minus the plugged-in estimates of the deviance using the means of the simulated parameter values to calculate p_D. Then DIC = $\bar{D} + p_D$. For example, at the kth iteration of a MCMC run, $D(\boldsymbol{\theta})$ is calculated for the models without AR(1) as follows:

$$\text{(B1)} \quad D(\boldsymbol{\theta}^{[k]}) = -2\log(f(y_{it}|\boldsymbol{\theta}^{[k]})) = \sum_{it} \log(2\pi(\sigma_i^2)^{[k]}) + (y_{it} - \mu_{it}^{[k]})^2/(\sigma_i^2)^{[k]}$$

DIC is very useful for comparing hierarchical models, where the number of parameters is not clearly defined. With nonhierarchical models, p_D is asymptotically the true number of parameters and DIC is thus equivalent to the more familiar Akaike information criterion (AIC).

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Bias in estimating food consumption of fish by stomach-content analysis

A. Rindorf and P. Lewy

Abstract: This study presents an analysis of the bias introduced by using simplified methods to calculate food intake of fish from stomach contents. Three sources of bias were considered: (1) the effect of estimating consumption based on a limited number of stomach samples, (2) the effect of using average contents derived from pooled stomach samples rather than individual stomachs, and (3) the effect of ignoring biological factors that affect the evacuation of prey. Estimating consumption from only two stomach samples yielded results close to the actual intake rate in a simulation study. In contrast to this, a serious positive bias was introduced by estimating food intake from the contents of pooled stomach samples. An expression is given that can be used to correct analytically for this bias. A new method, which takes into account the distribution and evacuation of individual prey types as well as the effect of other food in the stomach on evacuation, is suggested for estimating the intake of separate prey types. Simplifying the estimation by ignoring these factors biased estimates of consumption of individual prey types by up to 150% in a data example.

Résumé : Nous présentons une analyse des erreurs causées par l'utilisation de méthodes simplifiées pour calculer l'ingestion de nourriture à partir de contenus stomacaux chez les poissons. Nous avons examiné trois sources d'erreur, soit les conséquences (1) d'estimer la consommation à partir d'un petit nombre de prélèvements de contenus stomacaux, (2) d'utiliser des contenus stomacaux moyens obtenus par le regroupement de prélèvements, plutôt que des prélèvements individuels et (3) de ne pas tenir compte des facteurs biologiques qui affectent l'évacuation des proies. Dans une étude de simulation, l'estimation de la consommation à partir de seulement deux prélèvements stomacaux a donné des résultats proches de l'ingestion réelle. En revanche, l'estimation de l'ingestion de nourriture à partir de prélèvements stomacaux regroupés introduit une erreur positive importante. Nous fournissons une correction qui peut servir à rectifier cette erreur dans l'analyse. Nous suggérons une nouvelle méthode, qui tient compte de la répartition et de l'évacuation des divers types individuels de proies, ainsi que de l'effet de la présence d'autres aliments dans l'estomac sur l'évacuation, pour estimer l'ingestion particulière des différents types de proies. La simplification de l'estimation par la négligence de ces facteurs produit une erreur dans la consommation estimée de proies individuelles pouvant atteindre 150 % dans un exemple basé sur des données réelles.

[Traduit par la Rédaction]

Introduction

The interaction between predatory fish and their prey is a key subject to be addressed when attempting to understand aquatic-ecosystem dynamics. The effect of the predator on the prey depends on the link between diet composition and prey availability and on the total amount of food ingested by the predator. Both diet composition and total consumption are frequently studied by combining knowledge of evacuation rates with field studies of stomach contents. Differing methods have been suggested for this, depending on the relationship between stomach contents and evacuation rate and on the assumption made concerning the progress of feeding between consecutive sampling points (Elliott and Persson 1978; Pennington 1985; Dos Santos and Jobling 1995). The evacuation of stomach contents of a number of fish species is well described by the relationship

$$\frac{dS(t)}{dt} = -\rho S^{\alpha}(t)$$

where ρ is the evacuation rate ($g^{1-\alpha} \cdot h^{-1}$), S is stomach contents (g), and α is a unitless constant (Jones 1974; Jobling 1981; Andersen 2001). If the predator ingests food at a rate $C(t)$ at time t ($g \cdot h^{-1}$), the stomach contents vary according to the differential equation

$$(1) \qquad \frac{dS(t)}{dt} = -\rho S^{\alpha}(t) + C(t)$$

This equation has been solved analytically for $\alpha = 1$ (exponential evacuation) in the case where $C(t)$ is constant over time (Eggers 1977; Elliott and Persson 1978). However, the equation does not have a general analytical solution and in many cases, food intake must be approximated numerically. In the case where α deviates from 1 and the intake rate is not necessarily constant, food intake is usually estimated by methods resembling that suggested by Pennington (1985), who estimated average hourly consumption in a sampling interval as

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A. Rindorf[1] and P. Lewy. Danish Institute for Fisheries Research, Charlottenlund Castle, DK2920 Charlottenlund, Denmark.

[1]Corresponding author (e-mail: ar@dfu.min.dk).

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$$(2)\qquad C_p = \frac{\rho}{N}\sum_{i=1}^{N} E(S_i^{\alpha}) + \frac{1}{T}[E(S(T)) - E(S(0))]$$

where C_p is the average food-intake rate ($g \cdot h^{-1}$) in the sampling interval, N is the number of sampling times in the sampling interval from time 0 to T h, $E(S(0))$ and $E(S(T))$ are the average stomach contents (g) of the population sampled at 0 and T h, respectively, and $E(S_i^{\alpha})$ is the average of the stomach contents to potency α (g^{α}) in the population sampled. $E(S(0))$ and $E(S(T))$ are estimated from the average stomach contents of the fish sampled at 0 and T h, from here on denoted $\bar{S}(0)$ and $\bar{S}(T)$, whereas $E(S_i^{\alpha})$ is estimated by $\frac{1}{M_i}\sum_{h=1}^{M_i} S_{i,h}^{\alpha}$, where M_i is the number of stomachs in the ith sample and $S_{i,h}$ is the contents of the hth stomach in the ith sample, from here on denoted S_i^{α} (Pennington 1985). Comparable methods have been suggested by a number of authors (Jones 1978; Armstrong 1982; Dos Santos and Jobling 1995), while others have used even simpler methods (Daan 1973; Lockwood 1980; Basimi and Grove 1985). The degree to which the estimates yielded by any of these methods are unbiased estimates of food-intake rate has hitherto only been investigated for $\alpha = 1$ (Eggers 1977; Elliott and Persson 1978; Héroux and Magnan 1996).

The calculation of consumption rate using eq. 2 in cases where $\alpha \neq 1$ requires information on the contents of single stomachs in order to estimate $E(S_i^{\alpha})$. However, the contents of all stomachs in a sample are often pooled at the time of collection to reduce the cost of examining composition. $E(S_i^{\alpha})$ is then estimated as $(\bar{S}_i)^{\alpha}$, where $\bar{S}_i$ denotes the observed average stomach contents in sample i (Jones 1978; Armstrong 1982; Patterson 1985). As can be shown using Hölder's inequality (Rao 1965), this procedure introduces a bias as $E(S_i^{\alpha}) < (E(S_i))^{\alpha}$ for $0 < \alpha < 1$. This bias has been noted by several authors (Ursin et al. 1985; Dos Santos and Jobling 1995; Andersen 2001), and is related to the proportion of stomachs that are classified as empty (Andersen 2001).

Predators with empty stomachs pose an additional problem, as these fish may be either caught in the interval between the evacuation of their last meal and the successful capture of the next prey, or not feeding for other reasons. When the average intake of the total predator population is estimated, the empty stomachs must obviously be included regardless of their origin. However, if only the intake of potentially feeding fish is desired, the individuals that are fasting for reasons other than the lack of successful capture of prey should be excluded. In the case of spawning fish, this can be done by excluding fish that are ripe or running, but generally the distinction between fasting individuals and feeding fish with empty stomachs is difficult to make, and this has led to the exclusion of empty stomachs prior to the estimation of food intake (Amundsen and Klemetsen 1988).

When the predator feeds on more than one prey species, the amount eaten of each prey type is often needed. This has been estimated by distributing the total intake among the different prey types according to the weight percentage of the prey in the total stomach contents (Armstrong 1982; Hawkins et al. 1985; Persson and Hansson 1999). The implicit assumption is that all prey types occur in the average amount in all stomachs and that the rates of evacuation of all prey types are equal. These assumptions are rarely, if ever, met (Dos Santos and Jobling 1995; Stefánsson and Pálsson 1997; Andersen 1999). Alternatively, the intake has been calculated for each prey type separately (Armstrong 1982; Patterson 1985). This allows the evacuation rate to be varied among prey types. However, the method does not take the effect of other food in the stomach into account. Calculating the intake in this way is therefore based on the assumption that only one prey type is present in each stomach or that evacuation of the prey is independent of other food in the stomach. This may hold in some cases (Magnússon and Aspelund 1997), but in many cases, each stomach contains several prey types (Rice 1988; Albert 1995) and these prey types are not evacuated independently of each other (Jones 1974; Andersen 2001). An exception to the assumption of separate evacuation of prey types is the equation given by Dos Santos and Jobling (1995). However, the parameters in their model have currently only been published for Atlantic cod (*Gadus morhua*) and furthermore, the model does not allow for changes in the average stomach contents over time.

This study presents an analysis of biases introduced by making simplifications and erroneous assumptions when estimating food intake. The investigation is divided into three parts: (1) an examination of the ability of the method suggested by Pennington (1985) to estimate food intake that occurs at a constant rate from two samples, (2) a study of the effect of using average stomach contents derived from pooled stomach samples to estimate food intake, and (3) an examination of the effect of ignoring biological factors that affect the evacuation of prey.

The difference between actual food intake and the estimate suggested by Pennington (1985) (part 1 above) is investigated in the case where the food-intake rate is constant and stomach contents are only sampled twice. The effects of the time elapsed between the sampling points and differences in evacuation rate on bias are examined. Further (part 2 above), an analytical expression for calculating an unbiased estimate of food intake directly from a pooled stomach sample is presented. Lastly (part 3 above), a new estimate of the intake of individual prey types is suggested. The estimate takes the distribution and evacuation of individual prey types into account as well as the effect of other food in the stomach on the evacuation rate. The bias introduced by ignoring these factors is analysed and exemplified by estimating the intake of English whiting (*Merlangius merlangus*) 25–30 cm in length caught at five different locations in the North Sea.

Analytical considerations

Bias in Pennington's method

The purpose of this exercise was to determine if Pennington's method provides an unbiased estimate of food intake when applied to a predator feeding at a constant rate between two sampling points. This was done by solving eq. 1 using numerical integration in a standard mathematical package for a number of combinations of known stomach contents at $t = 0$, $S(0)$, food-intake rate C, time interval T, and evacuation rate. The coefficient α was fixed at 0.5, as this value is appropriate for a number of fish species (Jobling

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1981; Andersen 2001). The numerical integration resulted in an estimate of the stomach contents at time T, denoted $S(T)$ below. Using this result, the ability of Pennington's approximation to estimate food-intake rate was determined by calculating

$$C_P = \frac{\rho}{2}\left(\sqrt{S(0)} + \sqrt{S(T)}\right) + \frac{1}{T}(S(T) - S(0))$$

The relative bias was calculated as

$$\frac{C_P - C}{C}$$

for each combination of $S(0)$, C, ρ, and T. Relative bias was estimated by for all combinations of $S(0)$ and C in the interval from 0.05 to 3.05 g. Evacuation rates of 0.04, 0.14, and 0.24 were used with a fixed time interval of 4 h to examine the effect of evacuation rate. These rates correspond to evacuation of slowly evacuated prey from whiting stomachs at 8 °C and of rapidly evacuated prey at 16 °C. The effect of the length of the interval between consecutive samples was examined by fixing the evacuation rate at 0.24 and estimating the difference for T = 1 h, T = 4 h, and T = 10 h.

Calculating an unbiased estimate of consumption from samples with a constant coefficient of variation

To obtain an estimate of $E(S_i^\alpha)$, $\hat{S}_i$, directly from the observed average stomach contents in a pooled sample, Andersen (2001) proposed a correction factor, κ, which should be multiplied to $(\bar{S}_i)^\alpha$:

$$\hat{S}_i^\alpha = \kappa(\bar{S}_i)^\alpha$$

The correction factor was calculated from a data set consisting of individually analysed saithe (*Pollachius virens*) stomachs by comparing $(\bar{S}_i)^\alpha$ and $\bar{S}_i^\alpha$. The factor was then applied to a data set consisting mainly of samples where the contents of the non-empty stomachs were pooled prior to weighing. However, if the distribution of the stomach contents follows a known distribution, the correction factor can be calculated analytically as well as numerically.

The distribution of the weights of the stomach contents has previously been shown to be reasonably described by delta distributions based on lognormal or gamma distributions (Aitchison and Brown 1957; Stefánsson and Pálsson 1997):

$$P(S = 0) = 1 - p$$

$$P(S \le s) = p\,\mathrm{LN}(s|\mu,\sigma^2), \quad S > 0$$

or

$$P(S = 0) = 1 - p$$

$$P(S \le s) = p\,\Gamma(s|k,\beta), \quad S > 0$$

where p is the probability that a stomach is not empty, $\mathrm{LN}(s|\mu, \sigma^2)$ and $\Gamma(s|k, \beta)$ are the distribution functions of a lognormal distribution with mean μ and variance σ^2 and a gamma distribution with shape parameter k and scale parameter β, respectively. In both cases, $E(S_i^\alpha)$ can be derived analytically and can be estimated by

$$\hat{S}_i^\alpha = \hat{p}_i\, e^{\alpha\hat{\sigma}_i^2(\alpha-1)/2}(\bar{x}_i)^\alpha \quad (3)$$

$$\hat{S}_i^\alpha = \hat{p}_i \frac{\Gamma(\hat{k}_i + \alpha)}{\Gamma(\hat{k}_i)\hat{k}_i^\alpha}(\bar{x}_i)^\alpha \quad (4)$$

(Appendix A) in the lognormal and gamma case, respectively, where $\bar{x}_i$ denotes the average contents of non-empty stomachs in the sample. If the coefficient of variation (CV) for the non-empty stomachs is constant, eqs. 3 and 4 reduce to

$$\hat{S}_i^\alpha = \hat{p}_i\, e^{\alpha\hat{\sigma}^2(\alpha-1)/2}(\bar{x}_i)^\alpha \quad (5)$$

$$\hat{S}_i^\alpha = \hat{p}_i \frac{\Gamma(\hat{k} + \alpha)}{\Gamma(\hat{k})\hat{k}^\alpha}(\bar{x}_i)^\alpha \quad (6)$$

in the lognormal and gamma case, respectively, where σ and k are the common parameters for all samples. These parameters must be estimated from stomachs analysed individually, preferably from a subsample of the data set. In the case of a constant CV, eq. 5 or 6 can then be used to estimate $E(S_i^\alpha)$ for samples where the contents of non-empty stomachs were pooled prior to weighing; $\hat{p}_i$ and $\bar{x}_i$ can be calculated from these samples, whereas σ_i or k_i is unknown. If a subsample is not available for estimating σ or k, the parameters could be estimated from a data set consisting of individually analysed stomachs sampled under similar conditions. It is readily apparent that the precision of eqs. 5 and 6 will depend on the degree to which the assumption of a constant CV is fulfilled. This assumption appeared to hold true for the contents of non-empty cod stomachs collected in restricted areas (Stefánsson and Pálsson 1997; Adlerstein and Welleman 2000). However, if an attempt is made to estimate the CV from other data sets, the validity of the assumption should be investigated further.

In addition to using eqs. 5 and 6 to correct for pooled samples, they can be applied in cases where stomachs were analysed individually but a common CV could be estimated for the entire data set. In this case, the simple average $\bar{S}_i^\alpha$ does not provide the best estimate of $E(S_i^\alpha)$, and eqs. 5 and 6 provide more precise estimates, as the information inherent in a common CV is taken into account.

The estimation of the variance of the estimated consumption has been described by Pennington (1985). However, if eq. 5 or 6 is used to estimate $E(S_i^\alpha)$, the equations do not apply. An estimate of the limits of the variance of consumption is given for both distributions (Appendix B).

The total consumption rate can be estimated by inserting eq. 5 or 6 into eq. 2. In the case of gamma-distributed non-zero stomach contents, α = 0.5, and a constant CV, the estimation is demonstrated in Table 1 (C_1). The corresponding estimate derived by simply substituting $(\bar{S}_i)^\alpha$ for $E(S_i^\alpha)$ is also given (C_2; Table 1). Assuming that $\bar{S}(0) = \bar{S}(T)$, the bias introduced by using C_2 rather than C_1 is

$$\frac{C_2 - C_1}{C_1} = \frac{\sum_{i=1}^{N}(p_i\bar{x}_i)^\alpha}{e^{\alpha\sigma^2(\alpha-1)/2}\sum_{i=1}^{N}p_i(\bar{x}_i)^\alpha} - 1 \quad (7)$$

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Table 1. Estimates of average hourly consumption.

Estimate	Calculation
C_1	$\frac{\rho_{tot}}{N}\sum_{i=1}^{N}\hat{p}_i\frac{\Gamma(\hat{k}_{tot}+1/2)}{\Gamma(\hat{k}_{tot})\sqrt{\hat{k}_{tot}}}\sqrt{\hat{X}_i}+\frac{1}{T}[\hat{p}(T)\hat{X}(T)-\hat{p}(0)\hat{X}(0)]$
C_2	$\frac{\rho_{tot}}{N}\sum_{i=1}^{N}\sqrt{\hat{p}_i\hat{X}_i}+\frac{1}{T}[\hat{p}(T)\hat{X}(T)-\hat{p}(0)\hat{X}(0)]$
$C_{3,j}$	$\frac{1}{N}\sum_{i=1}^{N}\sqrt{\hat{\pi}_{j,i}(\hat{\pi}_{j,i}\rho_j+(1-\hat{\pi}_{j,i})\rho_{res})\hat{p}_{j,i}}\frac{\Gamma(\hat{k}_j+1/2)}{\Gamma(\hat{k}_j)\sqrt{\hat{k}_j}}\sqrt{\hat{X}_{j,i}}+\frac{1}{T}[\hat{p}_j(T)\hat{X}_j(T)-\hat{p}_j(0)\hat{X}_j(0)]$
$C_{4,j}$	$\hat{\pi}_{tot,j}C_1$
$C_{5,j}$	$\frac{\rho_j}{N}\sum_{i=1}^{n}\hat{p}_{j,i}\frac{\Gamma(\hat{k}_j+1/2)}{\Gamma(\hat{k}_j)\sqrt{\hat{k}_j}}\sqrt{\hat{X}_{j,i}}+\frac{1}{T}[\hat{p}_j(T)\hat{X}_j(T)-\hat{p}_j(0)\hat{X}_j(0)]$

Note: See the text for an explanation of the notation.

in the case of lognormal-distributed contents of non-empty stomachs and

$$(8)\qquad \frac{C_2-C_1}{C_1}\approx\frac{\sum_{i=1}^{N}(p_i\bar{x}_i)^{\alpha}}{\frac{\Gamma(k+\alpha)}{\Gamma(k)k^{\alpha}}\sum_{i=1}^{N}p_i(\bar{x}_i)^{\alpha}}-1$$

in the case of gamma-distributed contents of non-empty stomachs. This bias was estimated for a number of combinations of p and k and p and σ, respectively, while α was held constant at 0.5; p was assumed to remain constant over the sampling period.

Estimation of the intake of individual prey types

Traditional estimates of prey-specific intake are based either on the distribution of total intake among prey types according to their weight percentages (Armstrong 1982; Hawkins et al. 1985; Persson and Hansson 1999) or on calculation of the intake of each prey type separately. The former method assumes that all prey types are present in the average amount in all stomachs and evacuated at the same rate, while the assumption of the latter method is that other food in the stomach has no effect on evacuation. Neither of these assumptions is generally met (Dos Santos and Jobling 1995; Stefánsson and Pálsson 1997; Andersen 2001). There is thus a need for an estimate that takes into account both the effect of the distribution and evacuation of individual prey types and the effect of other food in the stomach on evacuation.

A new estimate

The presence of other food in the stomach alters the evacuation of each particular prey type (Jones 1974), and the rate of evacuation of the total stomach contents lies within the range of rates for the individual prey types in the stomach (Andersen 2001). The proportion of all evacuated material that consists of a particular prey type is identical with the weight proportion of the prey in the stomach contents (Andersen 2001). In this study it will be assumed that the rate of evacuation of the total contents can be approximated by the average of the evacuation rates of the separate prey types weighted by the weight of each prey type, though this may not be entirely correct (Andersen 2001). The differential equation describing the evacuation of the total stomach contents is then

$$(9)\qquad \frac{dS_{tot}(t)}{dt}=-(\rho_j\pi_j(t)+(1-\pi_j(t))\rho_{res})S_{tot}^{\alpha}(t)+C_{tot}(t)$$

where $\pi_j(t)$ denotes the weight proportion of prey species j in the stomach at time t and S_{tot} denotes the total weight of food in the stomach. The parameters all refer to stomachs where prey type j is present, as the prey obviously does not affect evacuation in stomachs where it is absent; ρ_j is the evacuation rate of the prey in question and ρ_{res} is the evacuation rate of the other stomach contents (i.e., excluding prey type j). The differential equation describing the evacuation of prey type j becomes

$$(10)\qquad \frac{dS_j(t)}{dt}=-\pi_j(t)[\rho_j\pi_j(t)+(1-\pi_j(t))\rho_{res}]S_{tot}^{\alpha}(t)+C_j(t)$$

Recall that the proportion of the total amount of food evacuated that consists of prey type j is identical with the weight proportion of j in the stomach where the prey type occurs, i.e.,

$$\pi_j(t)=\frac{S_j(t)}{S_{tot}(t)}$$

Equation 10 can also be written as

$$(11)\qquad \frac{dS_j(t)}{dt}=-\pi_j^{1-\alpha}(t)[\pi_j(t)\rho_j+(1-\pi_j(t))\rho_{res}]\times S_j^{\alpha}(t)+C_j(t)$$

$\bar{C}_j$ can then be estimated by

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$$(12)\quad C_{3,j} = \frac{1}{N}\sum_{i=1}^{N} \pi_{j,i}^{1-\alpha}[\pi_{j,i}\rho_j + (1-\pi_{j,i})\rho_{res}] \times E(S_{j,i}^{\alpha}) + \frac{1}{T}(E(S_j(T)) - E(S_j(0))$$

(Table 1). The subscript 3 distinguishes this estimate from those obtained by other methods. This new estimate thus takes into account both the uneven distribution of prey types in the stomachs and the effect of other stomach contents on the evacuation of the particular prey type. $E(S_i^{\alpha})$ can be estimated directly from individually analysed stomachs or using eq. 5 or 6. In the latter case, an estimate of the occurrence of the prey type, p_j, is required as well as an estimate of σ_j or k_j.

Comparison of the new estimate with traditional methods

A number of authors estimate the intake of individual prey types by distributing the total intake according to the weight percentages of the different prey types (Armstrong 1982; Hawkins et al. 1985; Seyhan and Grove 1998):

$$(13)\quad C_{4,j} = \pi_{tot,j} C_1$$

where $\pi_{tot,j}$ is the weight percentage of prey type j in the contents of all stomachs and C_1 is the total food intake. This estimate is biased even in the case where both the evacuation rates and the CVs of the weight of the stomach contents are identical for prey type j and the total stomach contents (as shown in Appendix C). The effect on the bias of the proportion of stomachs that contain the particular prey type, p_j, relative to the probability that a stomach contains food of any kind, p_{tot}, and the effect of the ratio between the weight proportion of the prey type in all stomachs, $\pi_{tot,j}$, and in stomachs where the prey type occurred, π_j, was investigated in the special case where $\rho_j = \rho_{tot}$, $k_j = k_{tot}$, no change occurred in the average stomach contents over the sampling period, and $\pi_{tot,j}$ and π_j remain constant over the period. In this case, the relative bias is reduced to

$$(14)\quad \frac{C_4 - C_3}{C_3} = \left(\frac{\pi_{tot,j}}{\pi_j}\frac{p_{tot}}{p_j}\right)^{1-\alpha} - 1$$

(Appendix C). This bias was plotted as a function of the ratios $\frac{\pi_{tot,j}}{\pi_j}$ and $\frac{p_{tot}}{p_j}$ for $\alpha = 0.5$. The plot illustrates the bias introduced even in the case where the evacuation rate does not vary among prey types.

An alternative procedure is to calculate the intake of each prey type separately (Armstrong 1982; Patterson 1985). The assumption is that other food in the stomach has no effect on evacuation. The differential equation describing the stomach content then becomes

$$\frac{dS_j(t)}{dt} = -\rho_j S_j^{\alpha}(t) + C_j(t)$$

and food intake rate can be calculated as

$$(15)\quad C_{5,j} = \frac{\rho_j}{N}\sum_{i=1}^{N} E(S_{j,i}^{\alpha}) + \frac{1}{T}[E(S_j(T)) - E(S_j(0))]$$

The formula is thus identical with eq. 2, except that it refers only to the weight and evacuation rate of prey type j. If π_j remains constant over the period, the bias introduced by this method reduces to

$$(16)\quad \frac{C_{5,j} - C_{3,j}}{C_{3,j}} = \frac{\rho_j}{(\pi_j\rho_j + (1-\pi_j)\rho_{res})\pi_j^{1-\alpha}} - 1$$

(Appendix C). This bias was plotted as a function of ρ_{res}/ρ_j and π_j.

Materials and methods

Data set

The data were obtained from whiting 25–30 cm in length gathered around the clock at five locations in the North Sea. Trawl hauls were performed at 4-h intervals for a total of 48–72 h. The sampling procedure has been described in detail elsewhere (Rindorf 2002) as has the calculation of the occurrence and weight of different prey types (Rindorf 2003, 2004). The total weight present in non-empty stomachs and the occurrence of non-empty stomachs were analysed using models similar to the analyses of total weight and occurrence of a single prey type described in Rindorf (2003, 2004). Briefly, the effect of time of day, time elapsed since the first sample was taken, and location on occurrence and mean weight of single prey and total stomach contents was analysed. If a factor was found to have no significant effect on weight or occurrence, samples were joined prior to estimation of mean weight or occurrence, respectively. This procedure was used to minimize random errors in the estimates. The weight of both single prey and total stomach contents in stomachs where this exceeded zero was assumed to be gamma-distributed with a constant CV.

The average hourly food intake was calculated from the estimated average stomach contents in non-empty stomachs, the estimated common shape parameter, k, and the occurrence of non-empty stomachs, p. The estimation of these parameters was described in detail in Rindorf (2003, 2004).

The bias introduced by not correcting for the inequality between $(\bar{S}_j)^{\alpha}$ and $\bar{S}_j^{\alpha}$ was examined by estimating the total consumption as C_1 (correcting) and C_2 (not correcting) (Table 1). The bias introduced by the two simplified methods for calculating intake of individual prey was investigated by estimating the intake of three different prey types as C_3, C_4, and C_5 (Table 1). Benthic invertebrates were chosen as an example of a prey that was generally small, occurred frequently in the stomachs, and had a high evacuation rate. Atlantic herring (*Clupea harengus*) was chosen as an infrequent large prey with an evacuation rate close to that of the total stomach contents. Finally, crabs were selected to exemplify prey that occurred frequently and possess a hard exoskeleton and thus are evacuated at a low rate.

Estimation of evacuation rates, $\pi_{tot,j}$ and π_j

The evacuation rate is dependent on both temperature and predator and prey characteristics. Additionally, the evacuation rate has been found to vary with meal size in some cases (Garber 1983; Elliott 1991; Temming and Andersen 1994), but as this effect has been shown to be insignificant in other cases (Bromley 1987; Andersen 1998), it was not

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considered in this study. The estimation of evacuation rates is described in detail in Appendix D and the resulting values are given in Table 2. The percentage of the total stomach contents that consisted of each prey type, π_{tot_j}, was calculated for each location and time of day. In addition, the percentage of the stomach contents that was made up by prey type j in the stomachs where it occurred, π_j, was calculated for each prey type, location, and time of day. Therefore, π_j was assumed to be constant and statistically independent of S_j for a given time of day and location. As changes in S_j occurred through changes in p_j rather than in $\bar{x}_j$ (though trends in the former occurred over the sampling period, no trends were detected in the latter (Rindorf 2003, 2004)), this assumption appeared to be justified.

Results

Bias in Pennington's method

The bias was small for short intervals and in no case exceeded 3% when the time interval was 1 h. However, increasing the interval led to large differences when the stomach contents or intake was low (Fig. 1). The bias rose to +34% at a 10-h sampling interval and a very low food-intake rate. The difference between the two estimates increased with evacuation rate, being virtually zero for an evacuation rate of 0.04 (maximum bias –1.4%), rising to a maximum of 8% during a 4-h interval at an evacuation rate of 0.24 (Fig. 1). For the large majority of combinations of C and $S(0)$, the difference was less than 5% if the sampling interval was 4 h or less.

Calculating an unbiased estimate of consumption from samples with a constant CV

Substantial bias was introduced by estimating $E(\sqrt{S_i})$ as $\sqrt{S_i}$. The bias increased dramatically as a function of σ^2 and k^{-1} in the lognormal and gamma-distributed data, respectively (Fig. 2). Empty stomachs further increased the bias, leading to a maximum of several hundred percent in both distributions. The consumption calculated from the whiting data was increased by 51%, on average, when $E(\sqrt{S_i})$ was estimated as $\sqrt{S_i}$ (Table 3). The common shape parameter, k, of the distribution of the total stomach contents was 0.269 and the proportion of stomachs that contained food was around 0.8 (Table 3).

Estimation of prey-specific intake

Distributing the total intake among prey types according to weight percentage seriously biased the estimates (Fig. 3). The area in which the bias was less than 20% constituted a very small part of the possible parameter combinations. If the prey type was found in most of the non-empty stomachs, the bias was generally negative. As the occurrence of the prey type in the non-empty stomachs decreased, a positive bias became more likely. The data example demonstrated this, as the estimate $C_{4,j}$ was lower than $C_{3,j}$ when the prey type occurred frequently in the stomachs (Table 4). The estimate $C_{4,j}$ exceeded $C_{3,j}$ at low occurrences, particularly where the prey type constituted less than three-quarters of the stomach contents in the stomachs where it occurred. $C_{4,j}$ was biased by –36% and –44%, on average, for benthic invertebrates and crabs, respectively, when intake exceeded 3 mg·h^{-1}. Herring estimated by $C_{4,j}$ was positively biased at location 3, though the occurrence was similar to that at location 1, where a slight negative bias was found. This was caused by a higher mean weight of herring at location 3 (Appendix C).

Table 2. Rates of evacuation of total stomach contents and individual prey types in locations 1–5.

	1	2	3	4	5
Temperature (°C)	16.7	13.7	10.6	8.2	8.6
ρ_{tot}	0.120	0.098	0.087	0.075	0.077
$\rho_{benthic\ invertebrates}$	0.183	0.145	0.113	0.094	0.097
$\rho_{herring}$	0.160	0.127	0.099	0.082	0.085
ρ_{crabs}	0.091	0.072	0.056	0.047	0.048

Failing to include the effect on evacuation of other food in the stomach introduced a positive bias in consumption. When the prey type in question constituted half the weight of the stomach contents, consumption was estimated to be approximately 140% of the true consumption even when the rate of evacuation of the prey was identical with that of the total stomach contents (Fig. 4). However, as the prey type often constituted most of the stomach contents when it was present in the whiting stomachs, the positive bias in estimated consumption was only 26%, 9%, and 10%, on average, for benthic invertebrates, herring, and crabs, respectively (Table 4). The relative degree of bias in the three groups reflected that expected from the evacuation rate of the prey and the proportion of the stomach contents made up by this prey type (Table 4).

Discussion

The bias introduced by using Pennington's method to estimate a constant food-intake rate was very small for sampling intervals of 4 h or less. In contrast to this, simplifying the calculation of input data and making unwarranted assumptions regarding the distribution of prey in the stomachs led to serious bias in the estimated food intake.

The estimation of $E(S_i^n)$ by $(\bar{S}_i)^n$ led to substantial overestimation of consumption. This effect was also noted by Ursin et al. (1985), Dos Santos and Jobling (1995), and Andersen (2001) using different methods. The latter author estimated correction factors that could be applied to eliminate bias from data obtained from individually analysed stomachs. Though individual stomachs are also needed to estimate the parameters in the correction suggested here, the two methods differ in their underlying assumptions. Whereas Andersen's (2001) correction factor assumes a constant CV for the contents of non-empty stomachs as well as a constant proportion of empty stomachs, the present method allows these assumptions to be made indepeadently of each other, thus ensuring a minimum number of fixed parameters. Further, the method presented here provides a lower limit of the variance of the estimated consumption. The distribution and CV can be estimated from a subsample of the data set, and the remaining data can then be analysed by counting the empty and non-empty stomachs and recording the mean weight of

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Fig. 1. The bias introduced by using Pennington's method (eq. 2) to estimate a constant rate of food intake, showing the effect of evacuation rate at a 4-h sampling interval (*a* and *b*) and effect of the interval between sampling points at an evacuation rate of 0.24 (*b* and *c*). (*a*) $\rho = 0.14$ and $T = 4$; (*b*) $\rho = 0.24$ and $T = 4$; (*c*) $\rho = 0.24$ and $T = 10$. Relative differences are 0%–2%, 2%–4%, 4%–6%, 6%–8%, and above 8%, which are indicated by progressively darker shading. Positive differences are indicated by grids. The highest observed bias was 34% and the lowest was −15%.

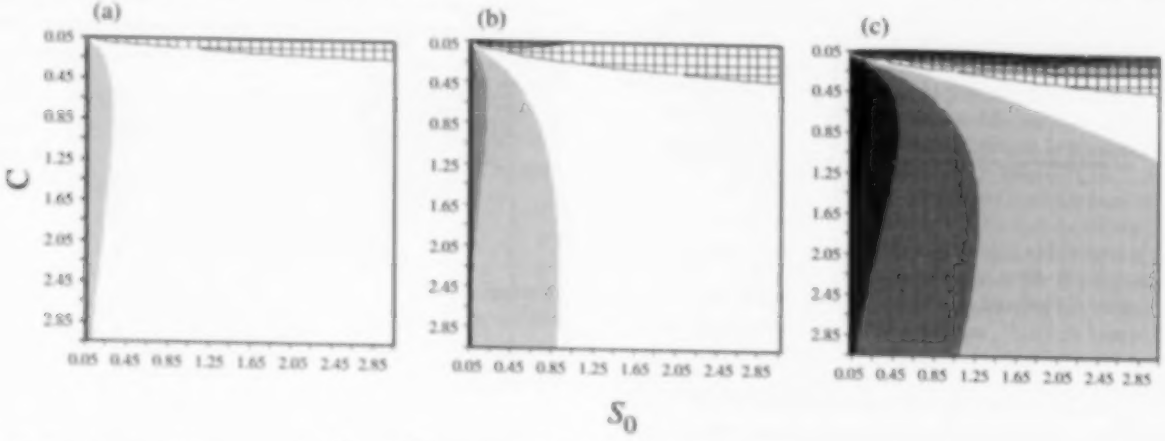
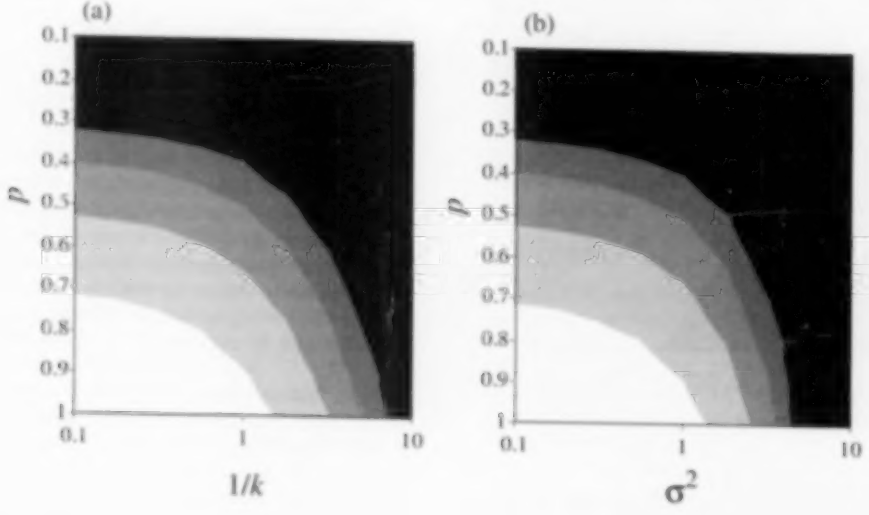


Fig. 2. Bias introduced by calculating $\sqrt{\hat{S}_i}$ as $\sqrt{\bar{S}_i}$ when X is (*a*) gamma-distributed and (*b*) lognormal-distributed as a function of the proportion of stomachs that contain food, p, and 1 divided by the shape parameter of the gamma distribution, k^{-1}, and the variance of the lognormal distribution, σ^2, respectively. The degrees of bias are 0%–20%, 20%–40%, 40%–60%, 60%–80%, and above 80%, which are indicated by progressively darker shading. The maximum recorded bias was 540% in the gamma-distributed case and 1000% in the lognormal-distributed case.



the contents of the non-empty stomachs. This sampling procedure has traditionally been followed in a number of stomach-sampling projects (International Council for the Exploration of the Sea 1988, 1991). The correction requires a constant CV, an assumption that may not hold if extensive areas or time scales are considered. There does, however, appear to be some evidence of constancy, as Stefánsson and Pálsson (1997) and Adlerstein and Welleman (2000) found evidence of a common CV for the contents of non-empty stomachs of Icelandic and North Sea cod, respectively. Nevertheless, the assumption is of crucial importance to the validity of the correction, and should be considered in detail before attempting to correct large numbers of samples.

Simply excluding empty stomachs leads to an overestimate of food intake, as the fish that were caught in the interval between the complete evacuation of their last meal and their successful capture of the next prey are excluded. Empty stomachs should only be excluded when there is biological evidence that these fish were indeed not part of the feeding population. In this study, there was no evidence that some predators may have been fasting. However, if some predators appeared to have decreased their food intake, because of

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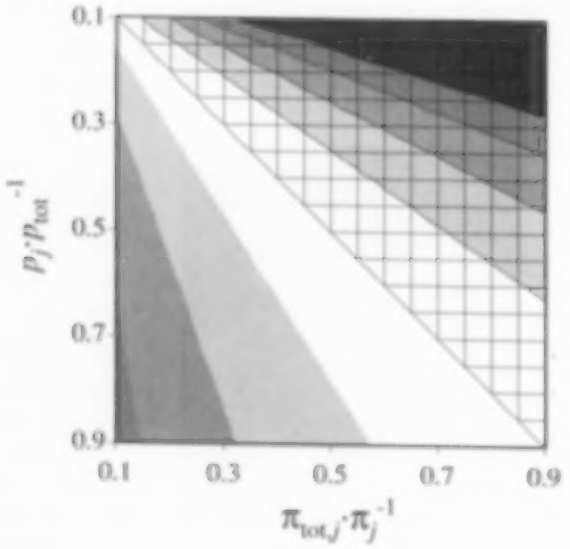
Table 3. Comparison of average food intake of whiting ($mg \cdot h^{-1}$) estimated by correcting for the fact that $E(S_i^{\alpha}) \neq (E(S_i))^{\alpha}$ (C_1) and by assuming $E(S_i^{\alpha})$ to be equal to $(E(S_i))^{\alpha}$ (C_2).

Location	C_1	C_2	$(C_2 - C_1)/C_2$	p^*
1	132	187	0.42	0.826
2	66	100	0.52	0.779
3	112	157	0.40	0.844
4	30	49	0.63	0.746
5	69	109	0.58	0.634

*The proportion of stomachs that contained food.

Fig. 3. Bias introduced by assuming that all prey types occur in all stomachs in the average amount $((C_{4,j} - C_{3,j}) \cdot C_{3,j}^{-1})$ as a function of the proportion of stomachs with food that contain prey type j, $p_j \cdot p_{tot}^{-1}$, and the ratio of the proportion of the prey type in the total stomach contents to the contents of the stomachs in which the prey type is found, $\pi_{tot,j} \cdot \pi_j^{-1}$. The degrees of bias are 0%–20%, 20%–40%, 40%–60%, 60%–80%, and above 80%, which are indicated by progressively darker shading. Positive differences are indicated by grids. The highest observed bias was 200%.



spawning, for example, the biologically most appropriate estimate of food intake would appear to be separate estimates for spawning and nonspawning fish; hence, empty and nonempty stomachs of spawning fish are considered together.

The new method for calculating the consumption of individual prey types yielded greatly improved estimates. Compared with this method, consumption of the three prey types considered was seriously biased by distributing the total consumption among prey types using weight percentages. Though the bias was generally negative, a positive bias was found for prey that occurred infrequently or constituted a minor part of the stomach contents when present. In general, larger fish prey occur in only a minor percentage of the stomachs collected (Albert 1995; Pillar and Barange 1997)

Table 4. Consumption ($mg \cdot h^{-1}$) of individual prey types at locations 1–5 estimated by three different methods, correcting for the unequal distribution of prey types and the effect of other food on evacuation ($C_{3,j}$), applying weight percentages to total consumption ($C_{4,j}$), and correcting for the unequal distribution of prey but neglecting the effect of other prey on evacuation ($C_{5,j}$).

	1	2	3	4	5
Benthic invertebrates					
Average π_j	0.72	0.81	0.67	0.73	0.68
Average p	0.23	0.39	0.40	0.08	0.02
Average X	0.74	0.74	0.74	0.74	0.74
$C_{3,j}$	17.2	37.0	24.2	3.7	1.3
$C_{4,j}$	7.1	32.6	16.1	2.3	3.2
$C_{5,j}$	22.4	41.6	31.1	4.7	1.7
Herring					
Average π_j	0.96	0.84	0.92	1.00	0.98
Average p	0.04	0.03	0.04	0.001	0.01
Average X	6.7	6.6	14.1	3.4	5.8
$C_{3,j}$	36.6	2.0	14.9	0.2	1.6
$C_{4,j}$	30.4	2.3	31.1	0.5	2.8
$C_{5,j}$	37.8	2.7	15.6	0.2	1.6
Crabs					
Average π_j	0.50	0.57	0.48	0.60	0.50
Average p	0.23	0.18	0.34	0.16	0.003
Average X	0.29	0.73	0.29	0.37	0.22
$C_{3,j}$	10.3	15.2	8.6	3.3	0.07
$C_{4,j}$	6.6	2.9	7.3	5.5	0.13
$C_{5,j}$	12.0	16.4	9.6	3.4	0.08

and so consumption of fish is likely to be overestimated, whereas that of invertebrates will be underestimated. This conclusion holds even when no difference in evacuation rate exists between the two prey types. Fish in which the evacuation of the stomach contents is exponential ($\alpha = 1$) represent a special case in which the error in distributing the total consumption according to weight percentages depends solely on the difference in evacuation rate between prey types (Appendix C).

The effect of other prey types on evacuation and hence consumption was minor in most cases. Only the intake of benthic invertebrates was biased to any extent by this assumption, and if simplifications of the calculations are to be made, making the assumption that each prey type is evacuated separately is far superior to distributing consumption according to weight percentages. Unfortunately, in studies calculating the intake of single prey types by this method, $E(S_i^{\alpha})$ is frequently estimated as $(\bar{S}_i)^{\alpha}$ (Armstrong 1982; Patterson 1985) and the results are therefore positively biased.

Estimating the intake of each prey type in the data set and summing these values to obtain the total intake led to estimates of total intake of 62%–131% of C_1 in the data analysed here. This difference may be the result of a combination of random errors and a tendency to overestimate the mean weight of highly digested prey, as prey in the last stages of digestion are not identified. However, the dif-

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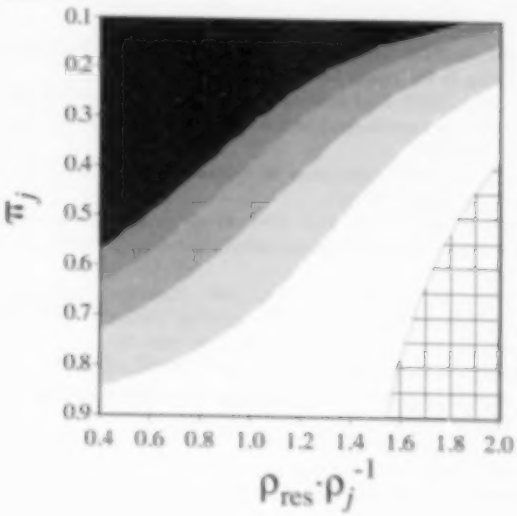
Fig. 4. Bias introduced by assuming that no other food is present in the stomach ($(C_{S,j} - C_{S,j}) \cdot C_{S,j}^{-1}$) as a function of the proportion of the stomach contents that consists of the given prey type, π_j, and the ratio of the evacuation rate of this prey type to that of the other stomach contents, $\rho_{res} \cdot \rho_j^{-1}$. The degrees of bias are 0%–20%, 20%–40%, 40%–60%, 60%–80%, and above 80%, which are indicated by progressively darker shading. The maximum recorded bias was 475%.



ference may also reflect a biologically more sensible method of calculation. Calculating an average rate of evacuation of the total stomach contents fails to account for any correlation between evacuation rate and weight of the stomach contents. Such a correlation may arise if the stomachs contain, for example, either small crustaceans (low evacuation rate) or large lean fish (high evacuation rate).

In addition to determining the effect of using different methods to estimate consumption, the present study demonstrates the importance of collecting samples throughout the diel cycle: the average intake of crabs estimated from daytime samples alone was only 25%–50% of that estimated from nighttime samples in the data at hand. This was connected to the primarily nocturnal feeding on crabs (Rindorf 2003). Sampling during the daytime only would therefore lead to gross underestimation of the total intake of this prey type.

The new method for calculating the intake of individual prey types has the advantage of incorporating the known sources of bias in estimates of food intake while allowing for change in the average stomach contents during the sampling period. A major disadvantage, however, is the expense of collecting detailed information on the contents of individual stomachs. If the CV is constant for each prey type, the required information could be limited to the average weight, the CV of this, and the occurrence of each prey type. The analyses of the stomachs would then not require the weighing of prey from each stomach individually, except for the subsample necessary to estimate the correction factor. The effect of other food in the stomach on estimated consumption appears to be minor in most cases.

In conclusion, the estimation of $E(S_i^{\alpha})$ as $(\bar{S}_i)^{\alpha}$ seriously biases the calculation of the food intake of fish. The bias increases with the variance of the contents of the non-empty stomachs and rises dramatically if the proportion of empty stomachs is high. Therefore, if data or CVs from single stomachs are not available, $E(S_i^{\alpha})$ should at the very least be estimated as $p_i(\bar{X}_i)^{\alpha}$, as this would eliminate the severe effect of empty stomachs. Distributing the total food intake among different prey types according to their weight percentage produces large biases, which may be either positive or negative according to the distribution and evacuation rate of the prey. As this bias can take any value, it is even more dangerous than the bias in the simplified calculations, as the latter is at least known to be positive. The results shown here once again stress the need for information on stomach contents at the single-stomach level. If this type of information cannot be obtained, great care should be taken to minimize the otherwise substantial bias.

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Appendix A. Estimation of $E(S_i^{\alpha})$ from $E(S_i)$.

Let the distribution of the weights of the stomach contents, S, be described by a delta distribution based on lognormal or gamma distributions (Aitchison and Brown 1957; Stefánsson and Pálsson 1997):

$$P(S = 0) = 1 - p$$

$$P(S \le s) = p\mathrm{LN}(s|\mu,\sigma^2), \quad S > 0$$

or

$$P(S = 0) = 1 - p$$

$$P(S \le s) = p\Gamma(s|k,\beta), \quad S > 0$$

where p is the probability that a stomach is not empty, $\mathrm{LN}(s|\mu, \sigma^2)$ and $\Gamma(s|k, \beta)$ are the distribution functions of a lognormal distribution with mean μ and variance σ^2 and a gamma distribution with shape parameter k and scale parameter β, respectively. In both cases, $E(S_i^{\alpha})$ can be derived analytically. Let the weight of the contents of a non-empty stomach be described by X, where X is lognormal distributed with mean μ and variance σ^2 of the log stomach contents:

$$X \in \mathrm{LN}(\mu,\sigma^2)$$

then

$$X^{\alpha} \in \mathrm{LN}(\alpha\mu,\alpha^2\sigma^2)$$

The relation between $(E(X))^{\alpha}$ and $E(X^{\alpha})$ is

$$E(X^{\alpha}) = e^{\alpha\sigma^2(\alpha-1)/2}(E(X))^{\alpha}$$

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and $E(S^\alpha)$ becomes

$$E(S^\alpha) = p e^{\alpha\sigma^2(\alpha-1)/2}(E(X))^\alpha$$

In the case of gamma distribution, $X \in \Gamma(k,\beta)$, $E(X^\alpha)$ is

$$E(X^\alpha) = \frac{\Gamma(k+\alpha)}{\Gamma(k)k^\alpha}(E(X))^\alpha$$

and

$$E(S^\alpha) = p\frac{\Gamma(k+\alpha)}{\Gamma(k)k^\alpha}(E(X))^\alpha$$

Hence $E(S_i^\alpha)$ can be estimated by

$$\hat{S}_i^\alpha = \hat{p}_i e^{\alpha\hat{\sigma}_i^2(\alpha-1)/2}(\bar{x}_i)^\alpha$$

$$\hat{S}_i^\alpha = \hat{p}_i \frac{\Gamma(\hat{k}_i+\alpha)}{\Gamma(\hat{k}_i)\hat{k}_i^\alpha}(\bar{x}_i)^\alpha$$

in the lognormal- and gamma-distribution case, respectively.

Appendix B. Estimation of the variance of the estimated consumption.

The variance of the estimated consumption can be estimated as

$$V(\hat{C}) = \frac{\rho^2}{N^2}\sum_{i=1}^{N} V(\hat{S}_i^\alpha) + \frac{1}{T^2}[V(\hat{S}(T)) + V(\hat{S}(0))]$$

in the case where $S(0)$ and $S(T)$ are not included in the summation and

$$V(\hat{C}) \cong \frac{\rho}{N^2}\sum_{i=1}^{N} V(\hat{S}_i^\alpha) + \frac{1}{T^2}[V(\hat{S}(T)) + V(\hat{S}(0))] + \frac{\alpha\rho}{N\cdot T}[(\hat{S}(T))^{\alpha-1}V(\hat{S}(T)) - (\hat{S}(0))^{\alpha-1}V(\hat{S}(0))]$$

in the case where $S(0)$ and $S(T)$ are included in the summation. To calculate this variance, estimates of the variance of $\hat{S}(0)$, $\hat{S}(T)$, and $\hat{S}_i^\alpha$ are needed. If it is assumed that σ and k are constant and known to be without error, the variance of $\hat{S}_i^\alpha$ can be approximated by

$$V(\hat{S}_i^\alpha) \cong e^{\alpha\sigma^2(\alpha-1)}[V(\hat{p}_i)(\bar{X}_i)^{2\alpha} + \alpha(\bar{X}_i)^{\alpha-1}V(\bar{X}_i)\hat{p}_i^2 + \alpha(\bar{X}_i)^{\alpha-1}V(\bar{X}_i)V(\hat{p}_i)]$$

and

$$V(\hat{S}_i^\alpha) \cong \left(\frac{\Gamma(k+\alpha}{\Gamma(k)k^\alpha}\right)^2[V(\hat{p}_i)(\bar{X}_i)^{2\alpha} + \alpha(\bar{X}_i)^{\alpha-1}V(\bar{X}_i)\hat{p}_i^2 + \alpha(\bar{X}_i)^{\alpha-1}V(\bar{X}_i)V(\hat{p}_i)]$$

in the lognormal- and gamma-distributed case, respectively.

However, as the values of σ and k are unlikely to be known exactly, these estimates have to be considered a lower limit. An overestimate of the variance of $\hat{S}_i^\alpha$ can, by analogy with Lewy (1996), be calculated as

$$V(\hat{S}_i^\alpha) \cong \frac{V(S_i^\alpha)}{M_i} = \frac{1}{M_i}\hat{p}_i(e^{2\hat{\mu}_i+\hat{\sigma}_i^2})^\alpha \times (e^{\alpha\hat{\sigma}_i^2(2\alpha-1)} - \hat{p}_i e^{\alpha\hat{\sigma}_i^2(\alpha-1)})$$

and

$$V(\hat{S}_i^\alpha) \cong \frac{V(S_i^\alpha)}{M_i} = \frac{1}{M_i}\frac{\hat{p}_i(\hat{k}_i\hat{\beta}_i)^{2\alpha}}{\Gamma(\hat{k}_i)\hat{k}_i^{2\alpha}}\left(\Gamma(\hat{k}_i+2\alpha) - \hat{p}_i\frac{(\Gamma(\hat{k}_i+\alpha))^2}{\Gamma(\hat{k}_i)}\right)$$

in the lognormal- and gamma-distributed case, respectively, in the case where σ or k is estimated for each sample separately. If a common estimate of σ or k is available, this estimate will be an upper limit, as the gain in precision obtained by estimating a common CV is not accounted for.

The variance of $\hat{S}(0)$ and $\hat{S}(T)$ can be approximated by

$$V(\hat{S}_i) \cong V(\hat{p}_i)(\bar{X}_i)^2 + V(\bar{X}_i)\hat{p}_i^2 + V(\bar{X}_i)V(\hat{p}_i)$$

The approximations given above can only be used when the variance of $\bar{X}_i$ and $\hat{p}_i$ can be estimated. They can therefore not be applied to pooled stomach samples. In this case, the variance can be approximated by

$$V(\hat{S}_i^\alpha) \cong \frac{V(S_i^\alpha)}{M_i} = \frac{1}{M_i}(e^{\alpha\hat{\sigma}^2(2\alpha-1)} - \hat{p}_i e^{\alpha\hat{\sigma}^2(\alpha-1)})\hat{p}_i\bar{X}_i^{2\alpha}$$

and

$$V(\hat{S}_i^\alpha) \cong \frac{V(S_i^\alpha)}{M_i} = \frac{1}{M_i}\frac{1}{\Gamma(\hat{k})\hat{k}^{2\alpha}}\left(\Gamma(\hat{k}+2\alpha) - \hat{p}_i\frac{(\Gamma(\hat{k}+\alpha))^2}{\Gamma(\hat{k})}\right)\hat{p}_i\bar{X}_i^{2\alpha}$$

in the lognormal- and gamma-distributed case, respectively.

The variance of $\hat{S}(0)$ and $\hat{S}(T)$ can be approximated by

$$V(\hat{S}_i) \cong \frac{V(S_i)}{M_i} = \frac{1}{M_i}(e^{\hat{\sigma}^2} - \hat{p}_i)\hat{p}_i\bar{X}_i^2$$

and

$$V(\hat{S}_i) \cong \frac{V(S_i)}{M_i} = \frac{1}{M_i}\left(\frac{\hat{k}+1}{\hat{k}} - \hat{p}_i\right)\hat{p}_i\bar{X}_i^2$$

in the lognormal- and gamma-distributed case, respectively. The precision of these estimates depends entirely on the adequacy of the assumption of a constant CV and the precision of the estimates of σ and k. They are further lower limits, as the variance of $\hat{\sigma}$ and $\hat{k}$ is not taken into account.

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Appendix C. Estimation of bias in traditional methods for estimating the intake of individual prey types.

The relative difference between the intake of prey type j calculated by the method presented here ($C_{\Sigma,j}$) and by multiplying the weight percentage of prey type j in the total stomach contents, $\pi_{\text{tot},j}$ by the total intake ($C_{\Delta,j}$) is

$$\text{(C1)}\quad \frac{C_{\Delta,j}-C_{\Sigma,j}}{C_{\Sigma,j}} = \frac{\pi_{\text{tot},j}}{\pi_j^{1-\alpha}}\frac{\rho_{\text{tot}}}{(\pi_j\rho_j+(1-\pi_j)\rho_{\text{exo}})}\frac{\sum_{i=1}^{N}E(S_{\text{tot}}^{\alpha})}{\sum_{i=1}^{N}E(S_i^{\alpha})}-1$$

where

$$\frac{\sum_{i=1}^{N}E(S_{\text{tot}}^{\alpha})}{\sum_{i=1}^{N}E(S_i^{\alpha})} = \frac{\frac{\Gamma(k_{\text{tot}}+\alpha)}{\Gamma(k_{\text{tot}})k_{\text{tot}}^{\alpha}}\sum_{i=1}^{N}p_{\text{tot},i}(E(X_{\text{tot},i}))^{\alpha}}{\frac{\Gamma(k_j+\alpha)}{\Gamma(k_j)k_j^{\alpha}}\sum_{i=1}^{N}p_{j,i}(E(X_{j,i}))^{\alpha}}$$

It is assumed that $\pi_{\text{tot},j}$ and π_j remain constant over the period and no change occurs in the average stomach contents over the sampling period. Note that in the special case $\alpha = 1$, the bias is entirely dependent on the difference in evacuation rate between prey.

If $\rho_{\text{tot}} = \rho_j = \rho_{\text{exo}}$ and $k_{\text{tot}} = k_j$, eq. C1 can be reduced by inserting $E(X_{\text{tot}}) = \frac{p_j}{p_{\text{tot}}}\frac{E(X_j)}{\pi_{\text{tot},j}}$:

$$\text{(C2)}\quad \frac{C_{\Delta,j}-C_{\Sigma,j}}{C_{\Sigma,j}} = \left(\frac{\pi_{\text{tot},j}}{\pi_j}\frac{p_{\text{tot}}}{p_j}\right)^{1-\alpha}-1$$

Once again it is evident that in the case of $\alpha = 1$, C_{Δ} is only biased if evacuation rates vary among prey types.

The bias introduced by disregarding the effect of other food in the stomach on evacuation (i.e., estimating food intake as $C_{\Sigma,j}$) is

$$\text{(C3)}\quad \frac{C_{\Sigma,j}-C_{\Sigma,j}}{C_{\Sigma,j}} = \frac{\frac{\rho_j}{N}\sum_{i=1}^{N}S_i^{\alpha}}{\frac{(\pi_j\rho_j+(1-\pi_j)\rho_{\text{exo}})\pi_j^{1-\alpha}}{N}\sum_{i=1}^{N}S_i^{\alpha}}-1 = \frac{\rho_j}{(\pi_j\rho_j+(1-\pi_j)\rho_{\text{exo}})\pi_j^{1-\alpha}}-1$$

It is again assumed that π_j remains constant and no change in the average stomach contents occurs over the sampling period.

Appendix D. Estimation of evacuation rates.

Andersen (2001) showed that the rate of evacuation of individual prey types without an exoskeleton is well described by a function of energy density of the prey. If several prey types occurred together, the rate of evacuation of the total stomach contents could be estimated from the average energy density of the total stomach contents (Andersen 2001). The relationship between evacuation rate and energy density was used here to calculate the rate of evacuation of prey without an exoskeleton. Energy densities were assumed to be equivalent to values given by Andersen (2001) and Pedersen and Hislop (2001). The energy density of benthic invertebrates was assumed to be 3.7 kJ·g^{-1} based on the evacuation rate given by Rindorf (2004). The evacuation rate of the total stomach contents at each location was then calculated as a weighted average of the evacuation rate of prey without an exoskeleton (calculated from the average energy density of these prey) and the evacuation rate of prey with an exoskeleton (taken to be equal to the value given for common (brown) shrimp (*Crangon crangon*) in whiting 27.5 cm in length by Andersen (2001)):

$$\rho_{\text{tot}} = (0.0025\pi_{\text{exo}} + 0.152E^{-0.86}(1-\pi_{\text{exo}}))e^{0.078\,\text{temp}}$$

where π_{exo} is the proportion of the stomach contents that consists of prey with an exoskeleton at each location, $1-\pi_{\text{exo}}$ is the proportion of the stomach contents that consists of prey without an exoskeleton, E is average energy density of the prey without an exoskeleton, and "temp" refers to the ambient temperature at the location. This is a modified version of the equation given by Andersen (2001) for whiting 27.5 cm in length. The sizes and temperature-specific evacuation rates, ρ_{LT}, of the three prey types were 0.00042 for benthic invertebrates (Rindorf 2004), 0.00021 for crabs (value given for common (brown) shrimp in Andersen 1999), and 0.00037 for herring (derived from the relationship given by Andersen (2001), and an energy density of 4.3 kJ·g^{-1} (Pedersen and Hislop 2001)). With a predator length of 27.5 cm, the evacuation rates were 0.050 $e^{0.078\,\text{temp}}$, 0.025 $e^{0.078\,\text{temp}}$, and 0.032 $e^{0.078\,\text{temp}}$ for benthic invertebrates, herring, and crabs, respectively.

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Inverse regional responses to climate change and fishing intensity by the recreational rockfish (*Sebastes* spp.) fishery in California

William A. Bennett, Kimy Roinestad, Laura Rogers-Bennett, Les Kaufman, Deb Wilson-Vandenberg, and Burr Heneman

Abstract: The interactive effects of ocean climate and fishing pressure on nearshore rockfishes (*Sebastes* spp.) were examined using historical commercial passenger fishing vessel catch records from California. Principal component analysis was used to characterize the dominant patterns in catch per unit effort (CPUE) over time (1957–1999) and space (10′ latitude × 10′ longitude blocks). Ocean climate explained 60% of the variation in CPUE and revealed opposite responses in northern and southern California. In warm El Niño years, CPUE was 4.2 times higher in the north and 1.8 times lower in the south. CPUE responded similarly to low-frequency climate shifts by increasing in the north and decreasing in the south after 1976–1977. Four geographic regions responded as discrete units to environmental forcing and fishing intensity: North, Central, South, and Channel Islands. Over time, annual fish landings declined sharply in the South, with fishing effort remaining stationary and high relative to that in the other regions. In the North, landings and fishing effort remained tightly coupled, with effort an order of magnitude lower than in the South. These findings support a management strategy for nearshore rockfishes in California based on regional responses to ocean climate and fishing intensity.

Résumé : Nous avons examiné les effets interactifs du climat océanique et de la pression de la pêche sur les sébastes (*Sebastes* spp.) de la région côtière en étudiant des données de pêche des années antérieures provenant des bateaux à passagers de pêche commerciale (« Commercial Passenger Fishing Vessels ») de Californie. Une analyse des composantes principales a servi à identifier les principales tendances des captures par unité d'effort (CPUE) dans le temps (1957–1999) et l'espace (des surfaces de 10′ latitude × 10′ longitude). Le climat océanique explique 60 % de la variation des CPUE; les réactions sont cependant opposées dans le nord et le sud de la Californie. Les années chaudes d'El Niño, les CPUE sont 4,2 fois plus élevés dans le nord et 1,8 fois plus bas dans le sud. Après 1976–1977, les CPUE réagissent de la même façon aux changements climatiques de faible fréquence en croissant dans le nord et en diminuant dans le sud. Quatre régions géographiques réagissent comme des unités indépendantes au forçage environnemental et à l'intensité de la pêche, soit les régions du nord, du centre, du sud et des îles Channel. Au cours des années, les débarquements annuels de poissons ont diminué de façon marquée dans le sud, malgré des efforts de pêche constants et élevés par comparaison aux autres régions. Dans le nord, les débarquements sont restés fortement liés à l'effort de pêche, alors que l'effort est 10 fois moindre que dans le sud. Ces observations appuient la mise en oeuvre d'une stratégie d'aménagement des sébastes côtiers de Californie basée sur leurs réactions régionales au climat océanique et à l'intensité de la pêche.

[Traduit par la Rédaction]

Introduction

Fishing pressure and climate change are primary drivers of interannual variability and long-term declines in many marine populations. While the ecological and socioeconomic consequences of overfishing are widely documented (Kurlansky 1997; Dayton et al. 1998; Pauly et al. 2002), we are just beginning to understand the confounding effects of interannual and interdecadal climate change (Glantz 1992; Beamish 1995; Bjørnstad and Grenfell 2001). Direct effects

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W.A. Bennett.[1] John Muir Institute of the Environment and Bodega Marine Laboratory, University of California – Davis, Box 247, 2099 Westside Road, Bodega Bay, CA 94923-0247, USA.
K. Roinestad and B. Heneman. Marine Life Management Project, Bolinas, CA 94924, USA.
L.Rogers-Bennett. California Department of Fish and Game, Bodega Marine Laboratory, University of California – Davis, Box 247, 2099 Westside Road, Bodega Bay, CA 94923-0247, USA.
L. Kaufman. Biology Department, Boston University Marine Program, Boston University, Boston, MA 02115, USA.
D. Wilson-Vandenberg. California Department of Fish and Game, Monterey, CA 93940, USA.

[1]Corresponding author (e-mail: wabennett@ucdavis.edu).

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of climate change on populations arise primarily from changes in sea temperature that can lead to reproductive impairment, recruitment failure, and shifts in distribution (Murawski 1993; Barry et al. 1995; Crawshaw and O'Connor 1996). Indirect effects on population abundances are typically attributed to complex changes in marine productivity and food-web dynamics (Francis and Hare 1994; Roemmich and McGowan 1995; Koslow et al. 2002). In many of these cases, however, obtaining evidence for bottom-up regulation of food webs depends on the quantity and quality of long-term monitoring information and the strength of statistical linkages between environmental and biological time series (Francis and Hare 1994; Koslow et al. 2002). This emphasizes the need to better understand the mechanisms underlying these direct and indirect pathways, as well as how they might interact with fishing pressure to undermine effective management (Hilborn et al. 1995; Dayton et al. 1998).

Many fisheries are severely depleted. Overfishing has occurred, in part, because management strategies did not recognize adverse climatic effects and adjust fishing pressure appropriately (Glantz 1992). This remains a problem even in well-understood systems. In data-poor fisheries, wide disparities in the amount and quality of long-term information will hamper efforts to decipher complex effects of climate change. In recognition of these limitations, as well as inherent uncertainties in forecasting, both fixed and variable management strategies have been proposed to accommodate unforeseen climate changes and their effect on fisheries (Walters and Collie 1988; Walters and Parma 1996; MacCall 2002). The extent to which each of these alternatives ameliorates climatic effects on fisheries depends on the underlying ecology of individual populations. For example, to withstand decadal-scale climate changes, long-lived species may benefit from a conservative fixed strategy that accounts for lower production, while a variable management strategy that more closely tracks environmental conditions appears to better suit short-lived species (MacCall 2002). Optimal management of fishery impacts will thus require strategies tailored to specific cases, raising the bar for investigators to identify key mechanisms of climatic effects (Walters and Collie 1988; Walters and Parma 1996; MacCall 2002).

In the Southern California Bight, it is generally recognized that a positive shift in the Pacific Decadal Oscillation (PDO; Mantua et al. 1997), coupled with frequent El Niño events, severally limited recruitment success in the rockfish (*Sebastes* spp.) fishery complex after 1976–1977. Warmer seas and reduced upwelling during this period are associated with dramatic declines in zooplankton abundance (Roemmich and McGowan 1995) and juvenile rockfish survival (Holbrook et al. 1997; Love et al. 1998*a*, 1998*b*). A concurrent weakening of the southward flow of the California Current also reduced larval-supply rates for several of the more commonly fished species near the southern boundaries of their ranges (MacCall 1996; Love et al. 1998*a*). The effects of climate change on recruitment, combined with intense fishing pressure on adults, probably contributed to declines in rockfish abundances in the Southern California Bight (Love et al. 1998*b*). Seven deep-water species are now considered overfished and severe fishing restrictions have been implemented (Ralston 2002). Similar signs of overfishing of shallow-water species have also been observed in central California (Mason 1995, 1998) and are suspected to exist statewide (Karpov et al. 1995). In the past, fishing regulations were implemented statewide, yet the ecology of many species, and socioeconomic characteristics, suggest that the fishery may benefit from management tuned to a finer regional scale. Climatic forcing may also operate at regional scales. Moreover, few studies have explored the historical contributions of fishing and climate changes in a common context or have defined the geographical scales at which regions may respond differently.

Here we examine simultaneous effects of climate change and fishing intensity in the nearshore recreational fishery for rockfish in California. The nearshore fishery, as defined by the California Department of Fish and Game (http://www.dfg.ca.gov/mrd/nfmp/index.html), is composed primarily of 19 shallow-water-dwelling fishes, including 13 of the more than 60 species of rockfishes (genus *Sebastes*) that occur in the eastern Pacific Ocean (Love et al. 2002). We use historical catch records from commercial passenger fishing vessels (CPFV) in concert with environmental data sources to test the working hypothesis that the California nearshore fishery responds in a geographically heterogeneous way to shifts in climate regime. If the null hypothesis (a homogeneous response among regions) is falsified, then management may need to recognize boundaries among regions that have responded as coherent units to climatic forcing and fishing pressure.

Methods

Data sources

The CPFV logbook records, administered by the California Department of Fish and Game, contain spatially explicit long-term records of fish landings by the California recreational charter boat, or party-boat, fishery. Since 1936, party-boat owners and operators have been required by law to record daily catch and location at which most fishing occurred. Locations are recorded using a grid of geographical blocks, 10′ latitude × 10′ longitude, encompassing the coastal Pacific Ocean off California (Fig. 1). We used monthly summaries of the CPFV records recently compiled by Hill and Schneider (1999) for 1936–1999 (with only annual summaries available for 1979). The CPFV data are known to contain several sources of reporting bias. These include irregular compliance and problems with accuracy (Karpov et al. 1995; Mason 1995, 1998). Consequently, we began our investigation under the assumption that such inaccuracies will be randomly distributed across the data when summarized at broad taxonomic, temporal, and geographical scales. Accordingly, we were restricted to using a generic rockfish category in our analyses because in most years all rockfish species are recorded as a single taxonomic group, and even when they have been broken out by species, some identifications are incomplete or suspect. In a few recent years and locations, various rockfish were categorized by species, and these records were pooled with the rockfish category.

To help focus our attention on trends in the nearshore fishery, we compiled seasonal and annual summaries of catch per unit effort (CPUE) for the two tiers of blocks closest to the coastline (Fig. 1). We examined data from the entire period 1936–1999; however, we confined multivariate analyses to

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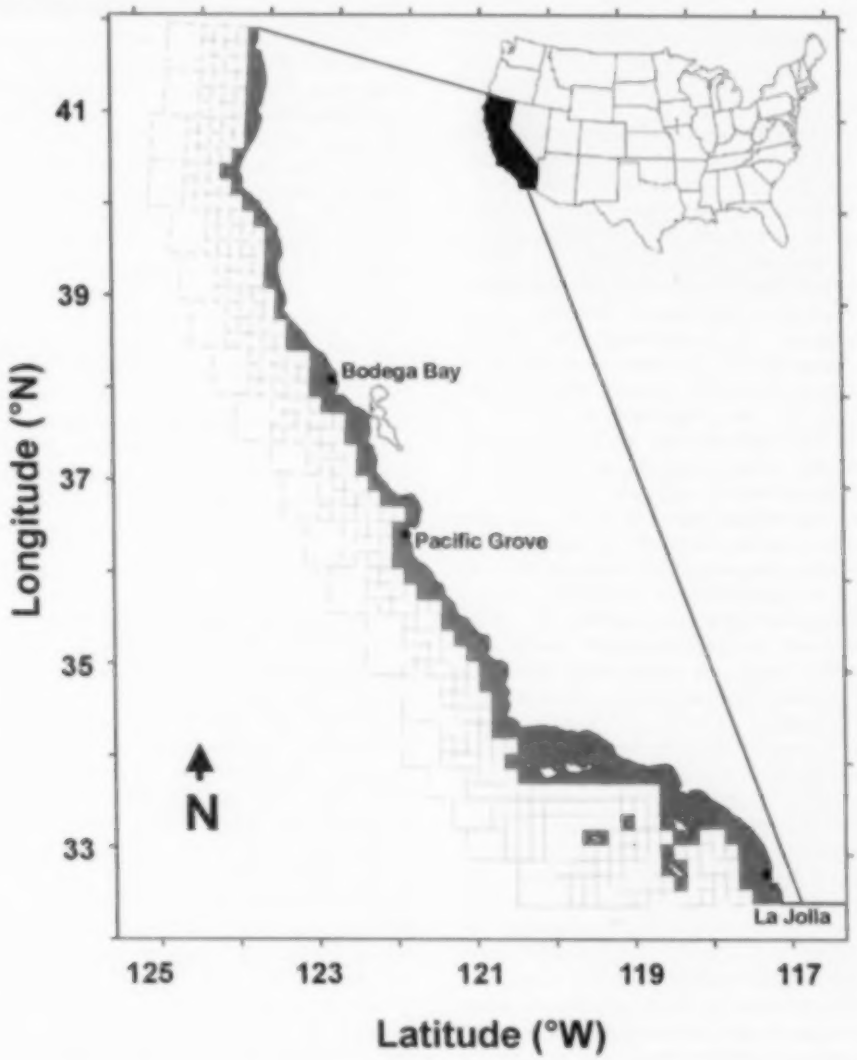
Fig. 1. Map of the California coastline showing the spatial grid of blocks (10′ latitude × 10′ longitude) used to report landings and effort (angler-hours) by commercial passenger fishing vessels (CPFV). The shaded blocks are those used in analyses for the nearshore component of the rockfish (*Sebastes* spp.) fishery. Also shown are the locations of the shoreline stations recording sea-surface temperatures at Bodega Bay, Pacific Grove, and La Jolla.



the years 1957–1999 because for previous years records are sparse north of Point Conception. Our measure of CPUE consisted of the total number of rockfish caught divided by the number of angler-hours, a measure of effort computed by multiplying the total hours fished by the number of fisherpersons on board (Hill and Schneider 1999). We further refined our effort measure by weighting the total number of angler-hours by the proportion of salmon (*Oncorhynchus* spp.), albacore (*Thunnus alalunga*), white seabass (*Atractoscion nobilis*), and California halibut (*Paralichthys californicus*) in the total catch. Few rockfish are caught when party boats target pelagic or sandy-bottom species. Therefore, this adjusted effort helped to account for annual and seasonal trends in the number of hours spent seeking other highly prized species that inflate effort with respect to rockfish landings.

We analyzed the CPFV data with several sources of environmental data that served as proxies for climate change. These included sea-surface temperatures (SSTs) and an index for the PDO. SST records from three shoreline stations located at Bodega Bay (Bodega Marine Laboratory), Pacific Grove (Hopkins Marine Laboratory), and La Jolla (Scripps Institute of Oceanography) were used to examine potential high-frequency temporal responses (e.g., El Niño) in different regions in northern, central, and southern California (Fig. 1). The PDO index was used to reflect potential low-frequency temporal responses (e.g., interdecadal) to regional climate change. Missing values in the Pacific Grove temper-

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ature records for 3 years (1975–1977) were supplied using temperatures from the Bodega Bay station adjusted upward by the long-term mean difference (2 °C) between these shoreline stations. Most of the SST and PDO index data were obtained over the internet at http://www-mlrg.ucsd.edu/shoresta/ and http://tao.atmos.washington.edu/pdo/.

Statistical analyses

We first explored the CPFV data with graphical methods on an annual and reporting-block basis, and then used principal component analysis (PCA) to summarize dominant patterns among the CPFV records over time (1957–1999) and space (blocks along the coastline). PCA examines patterns of covariance (or correlation) among variables in a matrix, and reduces multivariate data to a few uncorrelated indices, or principal components (Chatfield and Collins 1980). If excessive fishing pressure or extreme climatic events influence rockfish CPUE among years and locations, we might expect this variation to be partitioned among one or more principal components. We devised a tiered approach, using PCA on two forms of CPFV data matrices. For our initial analysis, we constructed a matrix using annual adjusted CPUE for blocks that consistently recorded rockfish landings. The columns of the matrix representing years (n = 43) and rows (n = 70) were reporting blocks. Then, PCA was computed from a covariance matrix. Because we were interested in uncovering potential causal mechanisms, we rotated selected components in n dimensional space (n = number of components) to identify modes of variation (Jassby 2000). We used the scree test method to select the major axes, defined as those principal components below and at the inflexion point in the slope of a cumulative-variance plot (Chatfield and Collins 1980). Each chosen component was then rotated using the orthogonal (varimax) and oblique (promax) methods. After rotation, we interpreted each mode by examining its factor loadings, or coefficients, which essentially measure the covariance between the original variables and a particular mode. In this case, the coefficients reflect interannual variation in CPUE. We also examined the mode scores, or amplitudes, which measure the relationship of each row element (or reporting block in this case) to each mode.

Because only the dominant mode of variation was readily interpretable, we devised a second PCA analysis in which we transposed and reduced the dimensions of the original matrix to facilitate interpretation of the modes of variation (Jassby et al. 1990; Jassby 2000). This dominant mode responded sharply to climate, therefore we condensed the initial matrix into regional-block groups according to a scheme based on latitudinal trends in CPUE between El Niño and La Niña years. This reduced the spatial dimension of the blocks into four distinct regions (North, Central, South, Channel Islands). We then used the monthly pattern of serial correlation in CPUE as a guide to define seasons (three seasons: January–April; May–August; September–December). This resulted in a 12 × 42 matrix, where the columns represent the CPUE for each of the three seasons and four regions, and the rows are years. As before, PCA from a covariance matrix was run and a scree graph was used to determine the number of principal components to be rotated using the varimax and promax methods. Now the coefficients associated with each mode would represent patterns of variation among regions and seasons, and the amplitudes would reflect temporal variation within regions and seasons for each mode.

To associate potential causal mechanisms with the modes of variation derived from the CPFV data, we first used graphical methods to explore the assumptions of various statistical models. We then used least-squares regressions if the assumptions were met by the data. If data did not fit the assumptions of normality and homoscedasticity we used generalized linear regression, and if they contained outliers we used robust regression, an iterative reweighting least squares procedure (Venables and Ripley 1997). Finally, we used multiple regressions to examine additive and interactive effects of environmental variables and fishing pressure. Residuals from model fits were examined for normality and autocorrelation. Significance levels were adjusted for models exhibiting autocorrelation in the residuals using the technique described by Pyper and Peterman (1998) that is robust to moderate levels of nonstationality in time series. Model fits between ordinary and multiple regressions were evaluated using Akaike's Information Criterion (AIC) that penalizes the log-likelihood of the residual sum of squares according to the number of fitted parameters (Burnham and Anderson 1998). All statistical analyses were performed using the S-PLUS statistical language (Venables and Ripley 1997).

Results

Following the initial PCA a scree plot of cumulative variance indicated that three principal components could be retained for rotation (Fig. 2). These three components explained 81% of the variation in CPUE, with 60% explained by the first component, 11% by the second, and 10% by the third. The results after rotation by the varimax and promax methods were similar, so here we present only the varimax solutions that retain an orthogonal orientation among modes (Chatfield and Collins 1980; Jassby 2000).

The time series of the coefficients for mode 1 reflect a strong climate-induced signal in CPUE (Fig. 3). Large coefficients correspond to El Niño years (e.g., 1983, 1992, 1997), whereas small coefficients correspond to La Niña years (e.g., 1971, 1974–1975) following year-type classifications by the National Oceanic and Atmospheric Administration Climate Prediction Center (http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.html). In addition, the coefficients increase overall after 1977, suggesting a response to the PDO (Mantua et al. 1997). Regressions using mode 1 as the dependent variable with annual mean SST from each shoreline location and the PDO index as independent variables were significant in all cases except for Pacific Grove (Table 1). This suggests that approximately 60% of the temporal variability in annual CPUE (mode 1) is associated with changes in ocean climate. However, temporal patterns in the coefficients for modes 2 and 3, as well as the mode amplitudes, were not readily interpretable.

Latitudinal trends in annual CPUE between El Niño and La Niña years showed distinct responses to climate change along the California coastline (Fig. 4*a*). CPUE is, on average, 4.2 times higher in El Niño years than in La Niña years in northern California (where the El Niño years were 1983, 1992, and 1998 and the La Niña years were 1971 and 1974–1975) when the means of three fitted lines are compared us-

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Fig. 2. Scree plot from principal components analysis of annual rockfish (*Sebastes* spp.) catch per unit effort (CPUE) from commercial passenger fishing vessel recording blocks along the California coastline. Variances (left-hand axis) are shown with cumulative variance (right-hand axis).

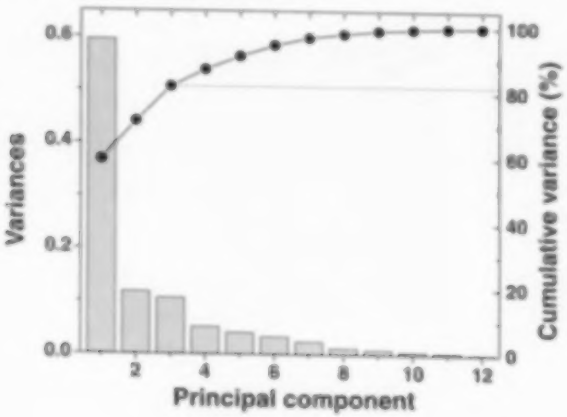
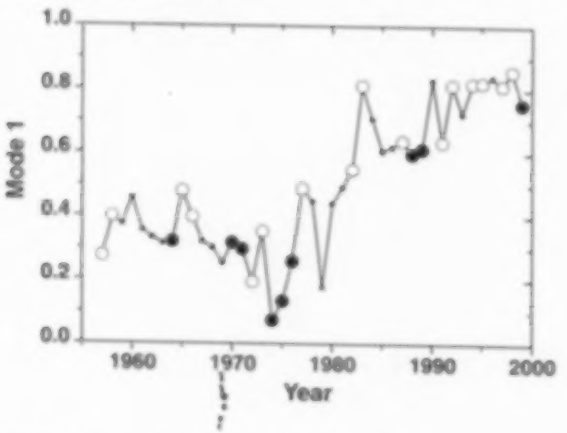


Fig. 3. Time courses of coefficients (loadings) for mode 1 determined from varimax rotation of the first three principal components. Also shown are loadings corresponding to El Niño years (○) and La Niña years (●).



ing local regressions (loess, degree = 1, fraction = 0.5; Cleveland 1993) (Fig. 4*b*). Conversely, CPUE is, on average, 1.8 times lower in warm-water years relative to cool-water years in southern California (south of Point Conception, recording blocks ≥651) (Fig. 4*b*). Central California (blocks ≥454, ≤643), ranging from San Francisco Bay in the north to Point Conception in the south, appears to be a region of transition between these opposing patterns, so that the northern boundary fluctuates depending on the signature of particular climatic events (Fig. 4*b*). For example, during the 1983 El Niño, fishing success remained higher than that observed in cool-water years until Morro Bay (Fig. 4*b*). Maximum CPUE in the fishery also typically occurs at Morro Bay. Based on the points at which these fitted lines intersect and diverge between cool- and warm-water years, we defined boundaries separating three regional bins to be used in our final PCA analysis (hereinafter North, Central, and South). We also defined a fourth regional bin encompassing the Channel Islands to examine potential differences in the response of mainland and island fishing grounds.

Table 1. Regression results for the first principal component (mode 1) of catch per unit effort (CPUE) from commercial passenger fishing vessels versus sea-surface temperature (SST) at shoreline stations, and an index for the Pacific Decadal Oscillation (PDO).

Environmental variable	df*	Mean	SE	*P*†
SST-recording station				
Bodega Bay	21	0.19	0.06	<0.01
Pacific Grove	21	0.094	0.115	>0.2
La Jolla	11	0.25	0.05	<0.0001
PDO index	11	0.196	0.046	<0.01

*Effective degrees of freedom.
†Adjusted for autocorrelation.

A scree plot from the PCA analysis using the regional and seasonal matrix showed that the first three principal components again account for about 80% of the variation in CPUE, this time among regions and seasons. The first principal component explains 69% of the variation, with the second and third components explaining only 8% and 6%, respectively. These three components were rotated, and the coefficients of each mode of variation are displayed by region and season in eigenmaps to facilitate interpretation (Fig. 5) (Jassby et al. 1990; Jassby 2000). The coefficients for mode 1 are consistently high across seasons in the South and Channel Islands regions and low in the North region (Fig. 5*a*). The Central region again transitions between North and South. Mode 2 is the mirror image of mode 1, with the North region now exhibiting the highest coefficients (Fig. 5*b*). Coefficients for mode 3 show seasonal differences, indicating that patterns in CPUE are similar in the South and Channel Islands regions during winter and early spring and in the North in summer and early fall (Fig. 5*c*). Overall, the South and Channel Island regions reflect similar patterns of variation.

The amplitude time series confirm that the modes reflect distinct patterns of CPUE in each region (Fig. 5). A time series for CPUE averaged over the South region is nearly identical with that for the coefficients of mode 1 (Fig. 5*a*). Moreover, mode-2 coefficients clearly reflect temporal variability in North-region CPUE (Fig. 5*b*), while mode 3 describes Central-region CPUE (Fig. 5*c*). Mode-1 coefficients and South-region CPUE both appear unimodal, reaching a maximum in 1975 (Fig. 5*a*). Conversely, the temporal trend for mode 2 and North-region CPUE appears to contain a climate signal, with higher values occurring in 1977, 1983, and 1991–1992 (Fig. 5*b*). Mode-3 coefficients and Central-region CPUE, however, are highly variable. After adjusting for significant autocorrelation, regressions among environmental variables and trends in regional CPUE are significant at the <0.05 level in all cases except the Central and Channel Islands regions and the PDO index (Table 2). Regressions with regional SST, PDO index, and CPUE are positive in the North and Central regions, whereas they are negative in the South and Channel Islands regions (Table 2).

Patterns shown by time trends in seasonal CPUE are also opposite in the northern and southern regions and are gener-

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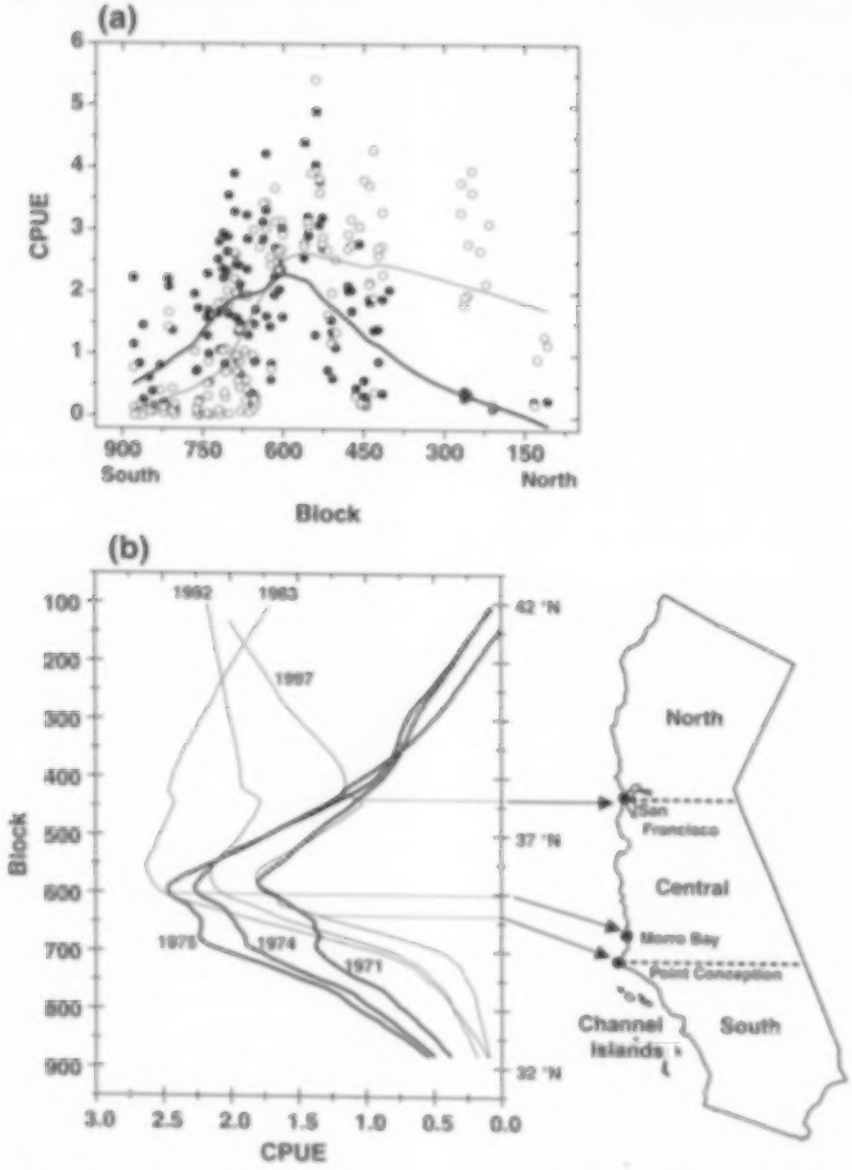
Fig. 4. (*a*) Annual CPUE for commercial passenger fishing vessel recording blocks along the California coastline in 1983 (El Niño year; thin line) versus 1974 (La Niña year; thick line), with local regression fits using loess (fraction = 0.5). (*b*) Loess fits to CPUE between 3 El Niño and La Niña years. Horizontal lines and arrows designate locations along the California coastline of maximum CPUE and key intersection points between trends in El Niño years (1983, 1992, 1997; thin lines) and La Niña years (1971, 1974, 1975; thick lines) used to define regional boundaries.



ally consistent with seasonal differences in SST (Fig. 6*a*). CPUE is consistently higher from May to December in the North and Central regions, although mean SSTs are only about 1 °C higher than those from January to April (Fig. 6*a*). In the South and Channel Islands regions, however, this pattern is reversed, with maximum CPUE occurring during the January–April season, when SSTs are about 2.5 °C lower than at other seasons (Fig. 6*a*). These seasonal patterns are also evident in the coefficients for mode 3 plotted in the eigenmap (Fig. 5*c*).

Interannual trends in levels of fishing effort and numbers of rockfish landed are distinct in each of the southern regions (Fig. 6*b*). In the South, CPFV records extend back to 1936, with a gap in reporting during World War II. The annual catch has averaged 463 000 rockfish, yet the trend is sharply bimodal, with a minor peak occurring in 1955 (about 900 000 fish) and a major peak in 1974 (about 1.6 million fish) (Table 3). Clearly, fish landings have plummeted in recent years (Fig. 6*b*). The trend in fishing effort, however, has remained stationary and high, averaging over 1 million

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Fig. 5. Eigenmaps showing space–time magnitudes of coefficients for three modes (*a*, *b*, *c*) determined from varimax rotation of three principal components. Space bins are regions along the California coastline, North (N), Central (C), South (S), and Channel Islands (CI), and time bins are seasons, January–April (S1), May–August (S2), and September–December (S3). Also shown are the time courses in the amplitudes (thick lines) with the mean CPUE (thin lines) from the South (*a*, mode 1), North (*b*, mode 2), and Central (*c*, mode 3) regions.

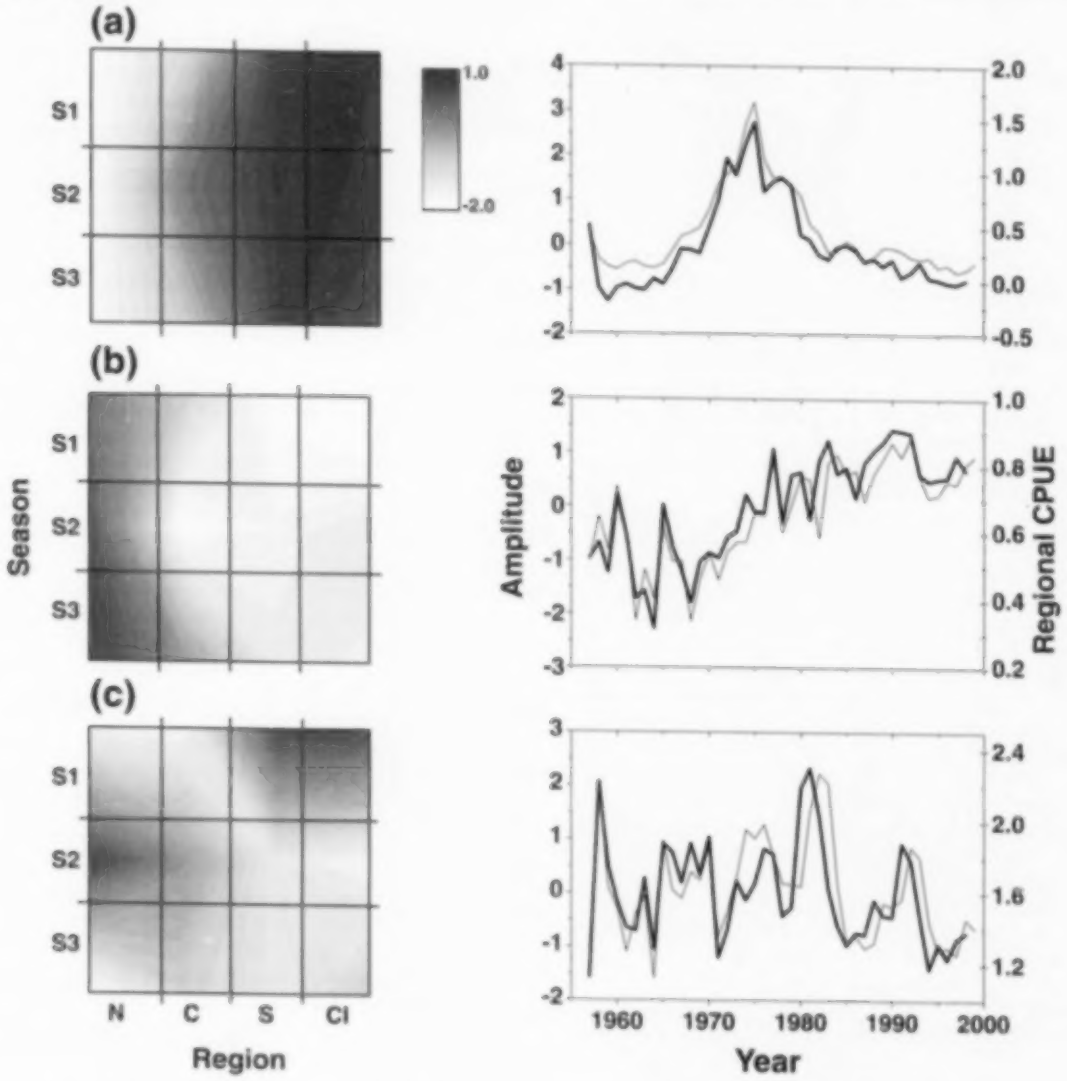

Table 2. Regression results for CPUE from commercial passenger fishing vessels in the North, Central, South, and Channel Islands regions versus SSTs from Bodega Bay (North), Pacific Grove (Central), and La Jolla (South and Channel Islands) shoreline stations and the PDO index.

	SST				PDO			
Region	df*	Mean	SE	P †	df*	Mean	SE	P †
North	22	0.075	0.035	<0.05	12	0.126	0.033	<0.01
Central	32	0.222	0.072	<0.01	28	0.038	0.058	>0.5
South	11	–0.227	0.038	<0.001	11	–0.167	0.056	<0.02
Channel Islands	18	–0.207	0.094	<0.05	18	–0.04	0.08	>0.5

*Effective degrees of freedom.
†Adjusted for autocorrelation.

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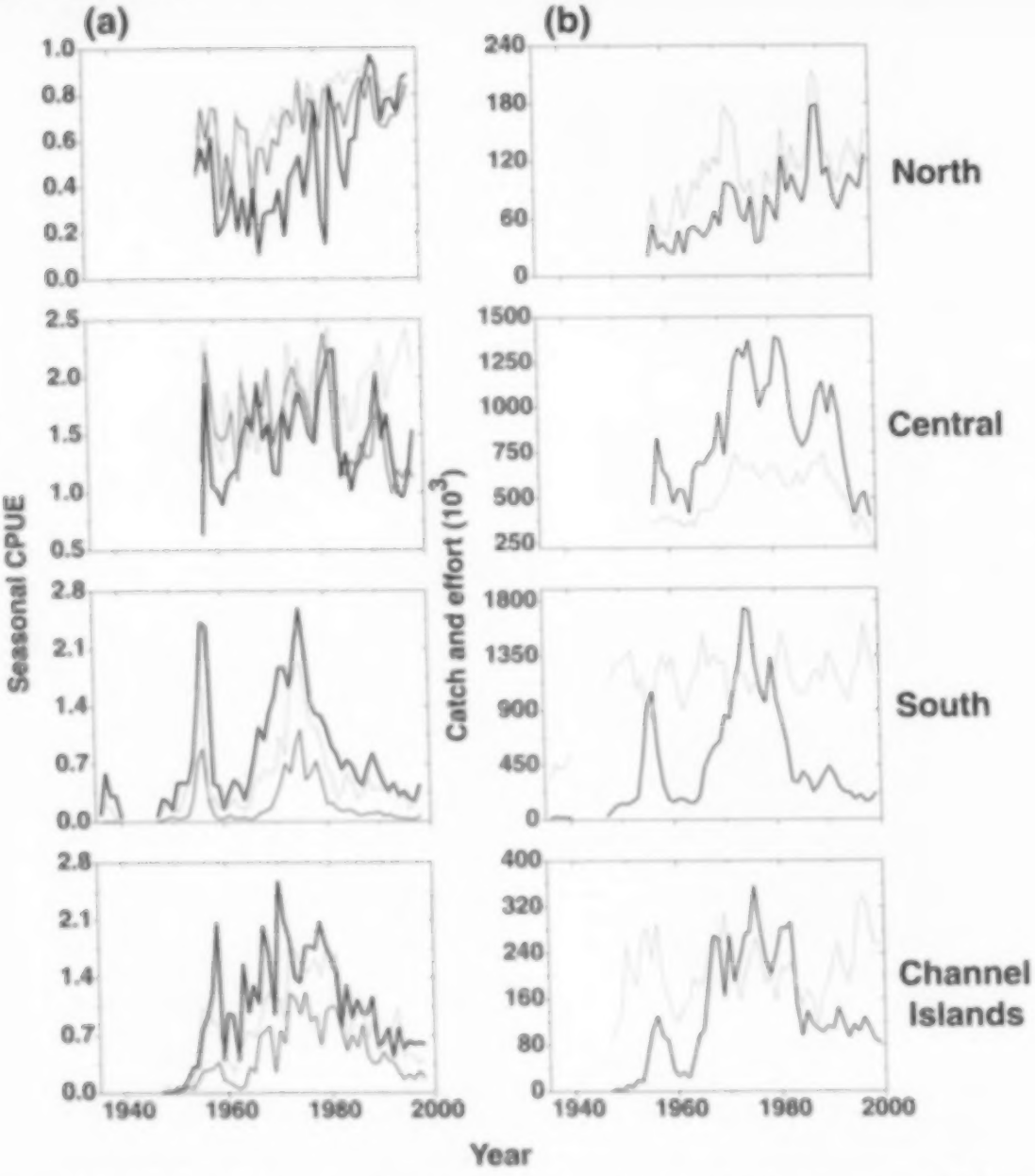
Fig. 6. (*a*) Temporal trends in rockfish (*Sebastes* spp.) CPUE among seasons, January–April (thick line), May–August (medium line), and September–December (thin line) and (*b*) rockfish landings (thick line) and fishing effort (angler-hours; thin line) in four regions along the California coastline.



angler-hours with irregular decadal cycling throughout the history of the fishery (Fig. 6*b*, Table 3). In addition, fishing effort has averaged about 2 h per kilometre of rockfish habitat as estimated by the extent of shoreline rocky habitat (National Oceanic and Atmospheric Administration 1995). The pattern in the Channel Islands is similar but with far fewer landings and less fishing effort (Table 3). Landings modestly track fishing effort until the late 1980s, but after this, landings decline despite a sharp upturn in fishing effort (Fig. 6*b*). Regressions show that the patterns in rockfish landings are unrelated to fishing effort in the South region; however, after autocorrelation is removed, a similar relationship in the Channel Islands region is close to the 0.05 significance level (Table 4). Multiple regression shows a negative and additive effect of fishing effort and SST on landings in the Channel Islands (Table 4). Both coefficients are significant and the model explains the pattern of landings better than fishing effort alone (lower AIC; Table 4). In the South region, SST by

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Table 3. Regional comparisons of key characteristics for the recreational rockfish (*Sebastes* spp.) fishery from commercial passenger fishing vessels.

Characteristic	North region	Central region	South region	Channel Islands region
No. of years	42	42	63	52
Year records begin	1957	1957	1936	1947
Mean effort	110	526	1100	209
Mean effort·km^{-1}	0.332	1.66	2.061	0.537
Maximum effort*	214 (1989)	746 (1990)	1620 (1997)	338 (1996)
Mean no. of landings	74	863	545	159
Mean no. of landings·km^{-1}	0.224	2.724	1.021	0.510
Maximum no. of landings*	174 (1990)	1387 (1981)	1741 (1974)	356 (1975)

Note: Effort is the number of adjusted angler-hours (10^3). Landings are the total number of rockfish reported for each region (10^3). Also shown are effort and landings per kilometre of rockfish habitat estimated from the amount of nearshore rocky habitat.
*The year is shown in parentheses.

itself also has a moderate ($P < 0.04$) negative effect on rockfish landings, as is also implied by comparisons of trends in latitudinal CPUE in warm- versus cool-water years (Fig. 4).

In contrast, patterns of fishing effort and rockfish landings in the North appear to be tightly coupled (Fig. 6*b*). Since logbook reports began in 1957, landings and effort have generally increased at a rate of about 2%·year^{-1} (Fig. 6*b*). Annual landings are highly associated with levels of fishing effort (Table 4); however, the relatively low level of average effort (110 000 angler-hours·year^{-1}) yields only about 75 000 rockfish·year^{-1} in this region (Table 3). Effort per kilometre of rockfish habitat has also averaged about 6 times lower than in the South region (Table 3). As before, the Central region exhibits trends that are intermediate between those in the North and South. Average annual landings (863 000 rockfish·year^{-1}) exceed that of the South, but with far less effort expended (mean = 526 000 angler-hours·year^{-1}), and about one-half of the effort expended per kilometre of rockfish habitat (Table 3). However, landings per kilometre of nearshore rockfish habitat have averaged about 2 times those in the South (Table 3). The trend in landings is similar to those in the southern regions; however, levels of fishing effort have also declined over the last decade (Fig. 6*b*), such that effort and landings are strongly associated, as in the North region (Table 4). Nevertheless, multiple regressions with fishing effort and either SST or the PDO index (the choice of variable to include was determined using the results in Table 2) show a strong positive and additive influence of ocean climate and fishing effort on numbers of rockfish landed (Table 4).

Discussion

Nearshore rockfish landings in northern and southern California respond to ocean climate in opposite ways. In the North, warmer ocean conditions increase the rate of fishing success relative to that in cool-water periods, whereas in the South, lower ocean temperatures increase CPUE. The Central coast appears to be a region of transition between these opposing patterns of climate-dependent fishing success. This response is apparent at both annual and seasonal time scales. These regions, as defined by the fishery response to climate, show dramatic differences in the potential impact of the fishery on rockfish landings, and share a southern boundary with the well-documented biogeographical division at Point Conception (Briggs 1974). Throughout the fishery record (1957–1999), rockfish landings closely track levels of fishing effort in the North, in contrast to the South, where landings were independent of fishing effort and remained an order of magnitude higher than in the North. This is also reflected by about 6 times more effort being expended per estimated kilometre of nearshore rockfish habitat in the South region. Such intense fishing effort may be partially responsible for the dramatic decline of landings in the South after the mid-1970s. In this respect as well, the Central region appears to be transitional. However, a higher number of landings per kilometre of nearshore rockfish habitat may imply that the Central region is more productive than the South. These results are consistent with previous findings showing declines in CPFV landings in the Southern California Bight, and in rockfish body lengths in the Monterey Bay area (Central region) (Mason 1998; Love et al. 1998*b*). Furthermore, our results show that fishing intensity and climate have an additive effect on rockfish landings in all regions except the South, where high effort may dominate the trends.

Regional responses by rockfish CPUE to climate change may be due to processes acting on fish foraging success, metabolic rates, and (or) appetites. This appears to be a unique mechanism involving both direct and indirect pathways of effect. Typically, climatic effects on fisheries are attributed to either direct effects on reproductive failure and physical effects on larval survival or indirect "bottom-up" effects on recruitment due to constraints on food-web productivity (Glantz 1992; Beamish 1995). These effects often exhibit time lags and do not manifest themselves until years later. Here we show how small changes (1–2 °C) in seasonal and annual mean temperatures exert immediate pronounced effects on rockfish CPUE at seasonal and annual scales. Similar adjustments in mean temperatures are sufficient to produce major changes in fish distribution and migration patterns (Crawshaw and O'Connor 1996). For example, increases of about 1 °C are associated with latitudinal shifts in distribution for 12 species in the western North Atlantic (Murawski 1993), as well as with earlier emigration dates for pink salmon (*Oncorhynchus gorbuscha*) from the Fraser River estuary (Henderson et al. 1995).

Responses to temperature combined with impacts from fishing suggest opposite scenarios for historical trends in different regions. In the North, lower food production and higher metabolic activity in warmer water may result in fish being hungrier and more active, rendering them more vulnerable to

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Table 4. Regression results for rockfish (*Sebastes* spp.) catch by commercial passenger fishing vessels versus adjusted fishing effort (angler-hours), SST, and PDO index by region in California.

Region	No. of terms	Independent variable	df*	Mean	SE	$P^{\dagger}$	AIC
North	1	Effort	15	0.837	0.062	<0.001	959.3
	2	Effort	23	0.839	0.053	<0.001	947.1
		PDO		11.23	2.835	<0.01	
Central	1	Effort	9	1.903	0.166	<0.001	1149.2
	2	Effort	24	1.913	0.154	<0.001	1143.9
		SST		103.2	37.91	<0.01	
South	1	Effort	13	–0.305	0.437	>0.3	1244.8
	1	SST	11	–303.6	83.29	<0.04	1233.2
Channel Islands	1	Effort	13	0.528	0.244	>0.05	1100.4
	2	Effort	24	0.585	0.223	<0.05	1093.2
		SST		–502.1	162.2	<0.02	

Note: La Jolla SST was used with the fishery data in the Channel Islands region. Akaike's information criterion (AIC) was used to compare model fits.
*Effective degrees of freedom.
†Adjusted for autocorrelation.

a set hook, thus increasing CPUE seasonally as well as during El Niños. Lower somatic and gonadal indices also have been reported for blue rockfish (*Sebastes mystinus*) in central California during these warm-water periods (Ven Tresca et al. 1995). Fishing in the North, however, may have been sustainable, perhaps related to lower overall effort due to a smaller human population and restricted access along a rugged shoreline, as well as frequently inhospitable ocean conditions. Sustainable fishing may also have occurred even though higher fishing effort was applied during warm-water years, when successful fishing may have increased the popularity of the fishery. In addition, lower ocean temperatures during years of average ocean conditions may have acted to dampen the rate at which fish were caught relative to other regions. Thus, the strong positive relationship between fishing effort, ocean temperature, and rockfish landings indicate that the fishery in the North, with more stable landings and CPUE, may have been sustainable at the regional scale over time. At smaller spatial scales, however, local depletions may have occurred, especially near fishing ports.

Conversely, in the South, warm-water effects on fish physiology may have dampened fishing success, but prolonged and intense effort may have overridden the temperature signal. SST during El Niños may approach unfavorable levels, such that nearshore species either decrease activity levels or move offshore to cooler water at depth, decreasing nearshore CPUE. Intense fishing during the initial stages of the fishery in the South region resulted in increased landings as is common in many fisheries. However, peak landings in 1974–1976 coincided with the well-documented shift in the PDO, which may have also reduced larval-supply rates (MacCall 1996). Subsequently, however, with no adjustment in fishing effort, landings may have declined as a consequence in the adverse climatic conditions (Love et al. 1998*b*). The dramatic collapse in landings, as well as reports of declines in fish body lengths and the proportion of adults in the catch (Love et al. 1998*b*), are indications that the South region may have been overfished.

Additional factors may have also contributed to the patterns observed in the CPFV data records. We have considered several confounding factors. First, although we attempted to emphasize the nearshore component of the fishery by confining our analyses to reporting blocks near the coastline, deeper water species were included in the generic rockfish category. The California Department of Fish and Game monitored rockfish catch on board CPFV vessels in the Central and North regions from 1987 to 1998, accompanying an average of 224 fishing trips each year (excluding 1987, 1990, and 1991, when fewer than half this number were monitored). Species identified in the catch show that proportions of nearshore rockfish varied regionally and among years, composing, on average, 75% in the North but only 45% in the Central-region reporting blocks used in our study (Fig. 7). Second, changes in fishing regulations and technological improvements throughout the historical record may also have influenced our results. The daily limit for rockfish per angler was 15 throughout most of the 43-year record; before 1971 it was 20 fish, and in 1999 it was lowered to 10 fish. Fishing technology, however, improved considerably over time, especially with the advent of hydroacoustics. These developments undoubtedly improved effectiveness, and impart a positive weighting on effort over time. Finally, other components of the nearshore fishery, such as private skiffs and the new commercial live-fish fishery, are not included in this analysis. The live-fish fishery includes nearshore rockfish species, California sheephead (*Semicossyphus pulcher*), cabezon (*Scorpaenichthys marmoratus*), and California scorpionfish (*Scorpaena guttata*) (Rogers-Bennett 2002), and appears to be approximately one-third the size of the recreational CPFV fishery, taking an average of 1.6 million fish each year since about 1990. In the future, our results will be compared with information from other components of the fishery.

Regional responses of rockfish landings to climate change and fishing effort provide an opportunity to tailor management strategies for the recreational fishery. Currently, our ability to manage the nearshore fishery (http://www.dfg.ca.gov/mrd/nfmp/index.html) is severely constrained by the daunting and costly task of developing detailed stock assessments with limited data for 19 individual species. Given the

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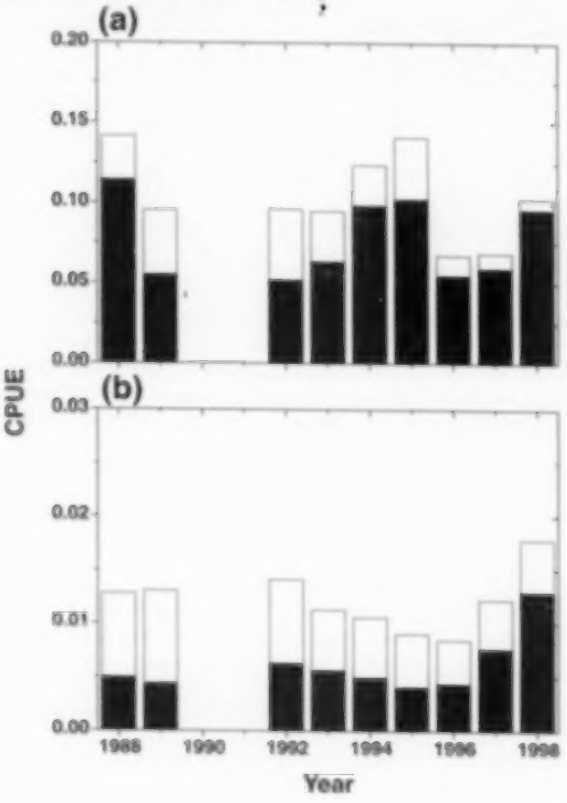
Fig. 7. CPUE for nearshore (solid bars) versus offshore (open bars) rockfish (*Sebastes*) species from commercial passenger fishing vessels in (*a*) the North and (*b*) Central regions. Rockfish identifications were conducted by onboard observers from the California Department of Fish and Game.



difficulties in using traditional management strategies based on virgin biomass, the regional responses to fishing pressure and climate described here may provide a framework for establishing a set of management procedures (Butterworth et al. 1997). Rules based on these regional responses may be devised to adjust total allowable catch, as opposed to setting a conservative fixed management strategy for the fishery statewide (Walters and Parma 1996; MacCall 2002). For example, we can now begin to identify excessive fishing pressure from levels in the South region (mean = 1.1 million angler-hours) that were unsustainable relative to fishing pressure in the North region (mean = 110 000 angler-hours), where the fishery appears sustainable. Moreover, rapidly evolving technology allows better monitoring of the progress of developing El Niños, providing a sentinel that permits managers to fine-tune fishing levels in near real-time, thus allowing for climatic effects on fish vulnerability. While no one can be certain how rockfish populations will respond to future fishing pressure and climate changes, the historical record suggests that cooler environmental conditions such as those occurring since 1999 (Durazo et al. 2001) may be beneficial to nearshore populations, particularly if rebuilding plans consider potential increases in southern fishing success that may occur as a result.

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PERSPECTIVE / PERSPECTIVE

Risk analysis of dissolved organic matter-mediated ultraviolet B exposure in Canadian inland waters

L.A. Molot, W. Keller, P.R. Leavitt, R.D. Robarts, M.J. Waiser, M.T. Arts, T.A. Clair, R. Pienitz, N.D. Yan, D.K. McNicol, Y.T. Prairie, P.J. Dillon, M. Macrae, R. Bello, R.N. Nordin, P.J. Curtis, J.P. Smol, and M.S.V. Douglas

Abstract: With depleted ozone levels and the possibility that climate change might lower dissolved organic matter (DOM) concentrations, the risk of exposure of fresh waters in Canada to ultraviolet B (UV-B) was evaluated. First, the distribution of a UV-B-sensitive zooplankton genus, *Daphnia*, was examined as a function of DOM concentration and maximum depth (Z_{max}) in 258 systems. Distribution was not restricted by UV-B, although very clear, shallow systems are underrepresented. Secondly, the depth at which 1% of surface radiance at 320 nm occurs ($Z_{320,1\%}$) was compared with Z_{max} in over 1000 aquatic systems in 15 ecozones to determine the proportions of optically clear systems ($Z_{max} \leq Z_{320,1\%}$) and systems that may become clear (i.e., are "at risk") should DOM decrease by 50%. South of the treeline, <6% of systems were clear, with the exception of two ecozones with 10%–20%. The proportion of systems at risk was 0% in most regions, with 5%–9% in four regions. DOM levels appear adequate to prevent extirpation of sensitive taxa like *Daphnia* through direct exposure to UV-B in most regions south of the treeline. However, optically clear and at-risk ponds were much more common in the three Artic ecozones, especially the Northern Arctic and Arctic Cordillera.

Résumé : Nous avons évalué le risque de l'exposition des milieux d'eau douce canadiens aux ultraviolets (UV-B), compte tenu des réductions de la couche d'ozone et de la possibilité que les changements climatiques réduisent les concentrations de matière organique dissoute (DOM). Nous avons d'abord examiné la répartition de *Daphnia*, un genre d'animal zooplanctonique sensible aux UV-B, en fonction de DOM et de la profondeur maximale (Z_{max}) dans 258 systèmes. La répartition n'est pas restreinte par l'UV-B, bien que les milieux peu profonds à eau très claire soient sous-

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L.A. Molot.[1] Faculty of Environmental Studies, York University, 4700 Keele Street, Toronto, ON M3J 1P3, Canada.
W. Keller. Cooperative Freshwater Ecology Unit, Ontario Ministry of the Environment, Laurentian University, Sudbury, ON P3E 2C6, Canada.
P.R. Leavitt. Department of Biology, University of Regina, Regina, SK S4S 0A2, Canada.
R.D. Robarts and M.J. Waiser. National Water Research Institute, Environment Canada, Saskatoon, SK S7N 3H5, Canada.
M.T. Arts. Aquatic Ecosystem Management Research Branch, National Water Research Institute, Burlington, ON L7R 4A6, Canada.
T.A. Clair. Atlantic Canada Region, Environment Canada, Sackville, NB E4L 1G6, Canada.
R. Pienitz. Département de Géographie, Université Laval, Québec, QC G1K 7P4, Canada.
N.D. Yan. Department of Biology, York University, Toronto, ON M3J 1P3, Canada.
D.K. McNicol. Environmental Conservation Branch, Ontario Region, Canadian Wildlife Service, Nepean, ON K1A 0H3, Canada.
Y.T. Prairie. Département des sciences biologiques, Université du Québec à Montréal, Montréal, QC H3C 3P8, Canada.
P.J. Dillon. Watershed Science Centre, Trent University, Peterborough, ON K9J 7B8, Canada.
M. Macrae. Department of Geography and Environmental Studies, Wilfrid Laurier University, Waterloo, ON N2L 3C5, Canada.
R. Bello. Department of Geography, York University, 4700 Keele Street, Toronto, ON M3J 1P3, Canada.
R.N. Nordin.[2] Water, Air and Climate Change Branch, British Columbia Ministry of Water, Land and Air Protection, Victoria, BC V8W 9M1, Canada.
P.J. Curtis. Earth and Environmental Sciences Department, Okanagan University College, Kelowna, BC V1V 1V7, Canada.
J.P. Smol. Department of Biology, Queen's University, 116 Barrie Street, Kingston, ON K7L 3N6, Canada.
M.S.V. Douglas. Department of Geology, University of Toronto, 22 Russell Street, Toronto, ON M5S 3B1, Canada.

[1]Corresponding author (email: lmolot@yorku.ca).
[2]Present address: Department of Biology, University of Victoria, Victoria, BC V8W 3N5, Canada.

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représentés. Ensuite, nous avons comparé la profondeur à laquelle se retrouve 1 % de la radiance de surface à 320 nm ($Z_{320,1\ \%}$) à Z_{max} dans plus de 1000 systèmes aquatiques dans 15 écozones, afin de déterminer le pourcentage de systèmes optiquement clairs ($Z_{max} \leq Z_{320,1\ \%}$) et de systèmes qui pourraient devenir clairs (donc à risque) si la concentration de DOM diminuait de 50 %. Au sud de la ligne des arbres, <6 % des systèmes sont clairs, sauf dans deux écozones où les pourcentages sont de 10–20 %. La proportion de systèmes à risque est de 0 % dans la plupart des régions, sauf dans quatre régions avec des pourcentages de 5–9 %. Les concentrations de DOM semblent suffisantes pour empêcher l'élimination de taxons sensibles, comme *Daphnia*, par exposition directe aux UV-B dans la plupart des régions au sud de la ligne des arbres. Cependant, les étangs clairs et les étangs à risque sont beaucoup plus nombreux dans les trois écozones arctiques, particulièrement dans le haut-arctique et la cordillère arctique.

[Traduit par la Rédaction]

Introduction

Many recent studies have investigated the effects of ultraviolet radiation (UVR; 290–400 nm) on aquatic systems. These have been stimulated in part by increases in summer solar radiation in the UV-B region (290–320 nm) associated with depletion of stratospheric ozone (e.g., see reviews in Hader 1997; de Mora et al. 2000; Helbling and Zagarese 2003). However, estimated increases in erythemal irradiance (a weighted UV-B function) since the early 1980s have only been about 6%–14% in Canada, depending on the region (Kerr et al. 2002). This suggests that ozone depletion is unlikely by itself to have resulted in widespread large-scale extirpation in aquatic systems unless key aquatic organisms are extremely sensitive to UV-B. A complicating factor, however, is that decreases in chromophoric dissolved organic matter (DOM), which strongly absorbs radiation in the UVR region (Scully and Lean 1994), could lead to significant increases in UV-B exposure. Two regional assessments of the risk posed by UV-B to amphibians in ponds in Minnesota and the US Northwest estimated that about 85% of ponds had adequate protection (Diamond et al. 2002; Palen et al. 2002; Peterson et al. 2002). There is, however, no clear picture of the extent, if any, to which the millions of lakes and ponds in Canada are at risk from UV-B exposure, a term defined operationally below.

Exposure to UV-B varies widely among aquatic systems, mainly because of variation in levels of DOM and its optical properties. It can range from less than 1 mg C·L^{-1} in exceptionally clear waters to more than 300 mg C·L^{-1} in some saline lakes in the Prairies (P.J. Curtis, unpublished data) (analytical methods for total organic carbon, i.e., high-temperature combustion and UV/persulphate methods, do not discriminate between chromophoric and non-chromophoric DOM). There is some concern that very large decreases in chromophoric DOM might occur as a result of reduced runoff associated with climate change (Leavitt et al. 1997; Schindler et al. 1997; Pienitz and Vincent 2000), producing large increases in underwater irradiance. In fact, increased UV-B exposure from reductions in chromophoric DOM might pose more of a risk to aquatic communities than ozone depletion (Williamson et al. 1996; Pienitz and Vincent 2000; Leavitt et al. 2003). On the other hand, counteractive processes associated with climate warming may affect northern lakes and raise their DOM concentrations (Clair et al. 1999). For example, with climate warming and an expected increase in vegetation at northern latitudes, e.g., the northern shift of the treeline, increased loads of DOM to lakes and ponds in these areas could occur (Pienitz and Vincent 2000). Attenuation of UVR by chromophoric DOM is discussed in more detail below.

Evaluating the extent to which aquatic environments might be "at risk" from UV-B exposure is warranted with the detection of harmful effects of UV-B on some taxa, the restoration of pre-industrial ozone levels still some years away, and the possibility that in chromophoric DOM concentrations might decrease significantly. We explore this topic for Canadian freshwater systems by first examining the eastern North American distribution of a crustacean zooplankton genus, *Daphnia*, which experimental evidence indicates may be a sensitive indicator of UV-B exposure. The first objective is to determine whether UV-B exposure restricts its distribution. Second, the maximum depth of UV-B transmission (defined here as the depth at which 1% of surface irradiance at 320 nm occurs ($Z_{320,1\%}$)) is compared with maximum depths (Z_{max}) for aquatic systems across Canada to determine the extent to which systems are currently optically clear or may become so (at risk) should they lose 50% of their DOM. Discussions of recent variation in incident levels of UV-B and the levels predicted over the short term (years) and long term (decades) across Canada are beyond the scope of this paper.

Methods

UV-B-sensitive indicator organisms

Rather than use the more subtle ecological changes that might occur, such as changes in life-history patterns or energy allocation to UV-protection mechanisms at the expense of growth, we chose instead to analyze the presence/absence of sensitive organisms. Research has shown that some stressors, such as acid deposition and Great Lakes contamination, have led to local extirpation in advanced stages of the problems, thus presence/absence data can be a practical tool for identifying severe damage. Moreover, because presence/absence data are more widely available than other ecological measurements, a larger number of systems can be assessed.

First, the literature was reviewed to identify sensitive indicator organisms. We then analyzed the presence/absence of the indicator taxa with respect to two relevant chemical and physical variables that affect the size of UV-B-free refuges, DOM concentration and Z_{max}, using several detailed synoptic surveys. The distribution of populations was compared with $Z_{320,1\%}$.

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Table 1. List of lake and pond surveys used to analyse dissolved organic matter distributions.

Ecozone	Province	Source[a]
Atlantic Maritime	Nova Scotia	Clair et al. 2001
	New Brunswick	T.A. Clair
Mixedwood Plains	Quebec (Townships)	Y.T. Prairie
Boreal Shield	Ontario	P.J. Dillon
	Ontario	D.K. McNicol
	Quebec (Abitibi)	Y.T. Prairie
	Newfoundland	Clair et al. 2001
Prairies		
Saline	Saskatchewan	Arts et al. 2000
Non-saline	Saskatchewan	Arts et al. 2000
Non-saline	Alberta	P.J. Curtis
Taiga Plains	Northwest Territories	Pienitz et al. 1997*a*
Hudson Plains	Manitoba	Macrae 1998
Taiga Shield	Northwest Territories	Pienitz et al. 1997*b*
	Northwest Territories	Rühland et al. 2003
Montane Cordillera	British Columbia	P.R. Leavitt
	British Columbia	R.N. Nordin
	British Columbia	Bos and Cumming 2003
Pacific Maritime	British Columbia	R.N. Nordin
Boreal Cordillera	Yukon	Pienitz et al. 1997*a*
Taiga Cordillera	Yukon	Pienitz et al. 1997*a*
Southern Arctic	Yukon, Northwest Territories	Pienitz et al. 1997*a*, 1997*b*
	Northwest Territories	Rühland et al. 2003
Northern Arctic	Nunavut, Northwest Territories	Antoniades et al. 2003
	Nunavut	Michelutti et al. 2002*a*, 2002*b*
	Nunavut	J.P. Smol and M.S.V. Douglas
Arctic Cordillera	Nunavut	Douglas et al. 2000

[a]Names of authors of this study are provided if the reference is not cited.

Several criteria were applied to the screening process. (*i*) Indicator organisms must be widely distributed among aquatic systems. (*ii*) Survival of indicator organisms must be impaired by UV-B and they must spend at least part of their life cycle in epilimnetic waters during summer daylight hours. For organisms to be useful as a biological indicator in this study, experimental evidence of sensitivity to UV-B must be coupled with evidence of changes in abundance. This is a practical consideration because only abundance data are likely to be widely available. (*iii*) Responses of indicator populations to UV-B change must be relatively rapid (time scale of weeks or months). (*iv*) Ideally, indicator organisms should play an important ecological role. (*v*) Chemical and physical indicators of UV-B exposure must be widely reported to ensure that an adequate number of lakes and ponds in various regions can be assessed.

Collectively, these criteria exclude process measurements such as primary-production and DOM-degradation rates, planktonic taxa at the species level (because of wide geographic variation and influence of non-UV-B-related factors), and long-lived taxa even where widely distributed (e.g., fish). Variation in nutrient loading with DOM loading (Dillon and Molot 1997) also precludes using a standing-crop indicator such as chlorophyll *a*. Certain experimental designs also preclude the use of their results in the search for indicators. For example, Bothwell et al. (1993) pointed out that "conclusions about the long-term ecological impacts of changes in UVB cannot be accurately forecast from short-term incubation studies". Furthermore, results of studies that remove UV-B through selective use of filters do not necessarily imply that a relationship between a response variable and UV-B intensity can be extrapolated to an increase in UV-B. Organisms must be exposed to UV-B levels above their "ambient" levels, perhaps by incubation in shallower waters or in waters with lower DOM concentration or by supplementation with an artificial source.

Distribution of systems at risk in Canada

DOM and Z_{max} data for aquatic systems across Canada were gathered from a variety of published and unpublished sources (Table 1). The surveys include mostly discrete (one time) measurements, although some means are included (e.g., the Nova Scotia and Newfoundland surveys provided long-term means), as long-term data are usually collected only from a small number of research sites. Z_{max} was not available from the Ontario Ministry of the Environment (OMOE) and Canadian Wildlife Service (CWS) Ontario surveys and was available for only some of the systems in the Arctic surveys. DOM was measured with either UV/persulfate digestion or high-temperature combustion.

$Z_{320,1\%}$ was compared with Z_{max} to determine the extent to which systems are currently optically clear or may become so (at risk) should they lose 50% of their DOM. $Z_{320,1\%}$ was chosen because deeper waters are virtually UV-B-free (see Attenuation of UVR penetration by chromophoric DOM below). Relative proportions of optically clear systems and

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Table 2. Regression equations for $\ln(K_\lambda)$ as functions of ln(DOM) and ln(POM) between 320 and 550 nm.

Eq.	λ (nm)	Intercept	Slope		R^2	$P > F$	
			ln(POM)	ln(DOM)		POM	DOM
4	550	–2.29	0.54	0.75	0.88	<0.0001	0.008
5	380	–0.35	0.42	1.03	0.92	<0.0001	0.014
6	360	–0.23	0.32	1.14	0.92	<0.0001	0.047
7	340	0.16	0.33	1.08	0.91	<0.0001	0.051
8	320	0.38	0.30	1.11	0.91	<0.0001	0.077

Note: Data are from Scully and Lean (1994). K_λ is the attenuation coefficient for wavelength λ, DOM is dissolved organic matter, and POM is particulate organic matter.

systems at risk were analyzed on a regional basis using the terrestrial ecozone classification adopted by Environment Canada in which 15 major ecosystems are defined on the basis of broad, common characteristics such as major plant formations (www.ccea.org/ecozones/terr.html).

The vast majority of the sampled sites (over 7200) were from two surveys of the Boreal Shield ecozone in Ontario (some sites were sampled in both surveys), with 791 sites sampled in 14 other ecozones across Canada. There are insufficient sampled sites from the Taiga Plains and Taiga Cordillera, with five and six sites, respectively. Hence, results for these ecozones should be treated with caution until additional data are available. Finally, some of the limnological surveys south of the treeline may have ignored small, shallow ponds (<1.0 m maximum depth), which could bias the results for regions where they are numerous. The exceptions to this are the Prairies survey of lakes and ponds in Saskatchewan, which includes 18 ponds (Arts et al. 2000), the CWS survey of lakes and ponds in the Boreal Shield in Ontario, which includes an unknown number of ponds (D. McNicol, unpublished data), and the Atlantic Maritime survey in Nova Scotia (six ponds) (Clair et al. 2001). By definition, a greater proportion of ponds than lakes should be at risk because of the shallow nature of the former.

Results

Attenuation of UVR Penetration by chromophoric DOM

The attenuation of incident radiation of a specific wavelength is described by exponential decay with depth:

$$(1) \qquad dE_{\lambda,Z}/dZ = -K_\lambda$$

$$(2) \qquad E_{\lambda,Z} = E_{\lambda,0}\exp(-K_\lambda Z)$$

where $E_{\lambda,Z}$ is the solar-radiation intensity at wavelength λ at depth Z below the surface, and K_λ is the attenuation coefficient for wavelength λ. The depth at which 1% of surface radiation for a given wavelength occurs (e.g., 99% attenuation) is given by

$$(3) \qquad Z_{\lambda,1\%} = -\ln(0.01)/K_\lambda = 4.61/K_\lambda$$

K_λ is a function of photon absorption by water and its constituents and photon scattering by particles (Vincent et al. 2001). UV-B is strongly absorbed by chromophoric DOM relative to light in the visible region (400–700 nm) (Crump et al. 1999; Markager and Vincent 2000).

The effect of chromophoric DOM and particulate matter on attenuation of solar radiation is illustrated with stepwise regressions developed using K_λ and DOM and particulate organic matter (POM) data for 14 lakes along a latitudinal gradient between 41 and 51°N (from Scully and Lean 1994). Attenuation coefficients for six wavelengths are reported between 300 and 400 nm. The attenuation coefficient at 550 nm was estimated by extrapolating the linear relationship between λ and $\ln K_\lambda$ for each lake. Regressions for attenuation coefficients at 320, 340, 360, 380, and 550 nm as functions of DOM and POM concentrations are shown in Table 2. These equations are used in the risk-assessment sections that follow. We make several assumptions here: (*i*) the relationship between $\ln K_\lambda$ and λ is linear between 300 and 550 nm within each lake, (*ii*) POM is an indicator of the level of suspended sediments, and (*iii*) the ratio of coloured to uncoloured DOM is relatively constant among the 14 lakes, though this is not strictly true for coloured Precambrian Shield waters (Molot and Dillon 1997*a*). A fuller discussion of the latter is included below.

Irradiance in the visible region penetrates much deeper than irradiance in the UV-B region at all concentrations of total organic matter (TOM = DOM + POM). $Z_{320,1\%}$ exceeds 6 m when TOM < 2 mg C·L^{-1} and is restricted to depths <1 m when TOM > 7 mg C·L^{-1}. $Z_{550,1\%}$ exceeds 70 m when TOM < 2 mg C·L^{-1} and is restricted to depths <13 m when TOM > 7 mg C·L^{-1}. Note that the depth of relative penetration depends only on the absorption and scattering properties of the water body and not on absolute irradiance, whereas absolute irradiance depends on absolute surface irradiance, as well as the absorption and scattering properties. A decrease in DOM will therefore significantly affect irradiance at a given depth at constant surface irradiance. For example, if DOM in a lake declines from 3 to 2 mg C·L^{-1} with 0.2 mg C·L^{-1} POM, then K_{320} will decrease from 3.05 to 1.95 m^{-1}, $Z_{320,1\%}$ will increase from 1.51 to 2.36 m and the irradiance at 320 nm at 1.51 m will increase 5.3-fold. Similarly, the irradiance at 300 nm at 1.51 m will increase 1.23-fold, an increase much larger than the estimated increase of 6%–14% in erythemal UV-B (Kerr et al. 2002).

Analysis of *Daphnia* presence/absence as a function of DOM and Z_{mix}

A review of studies of UV-B-impact studies on amphibians, fish, phytoplankton, zooplankton, macrophytes, and littoral-zone algae suggests that there is only one indicator so far that meets all of the criteria. Species of the cladoceran crus-

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Table 3. Summary of lakes and ponds from four surveys with maximum depth < 17 m and DOM < 5 mg C·L^{-1} used to analyze *Daphnia* distributions.

Source	No. of lakes and ponds	Region
Norman Yan, Ontario Ministry of the Environment[a]	18	Muskoka–Haliburton, Ontario
Bill Keller, Laurentian University[a]	151	Algoma and Sudbury, Ontario
Don McNicol, Canadian Wildlife Service[a]	8	Sudbury, Ontario
US Environmental Protection Agency Environmental Monitoring and Assessment Program, Eastern Lake Survey[b]	81	Northeastern USA

[a]DOM measured by acidifying samples, flushing with N_2 to remove inorganic C, then oxidizing with a UV digester in acid persulfate media. CO_2 is colorimetrically detected.

[b]Analytical method for DOM described in Hillman et al. (1986). Data are available on-line at www.epa.gov/docs/emap/html/datal/surfwatr/data/napap/els.html.

tacean genus *Daphnia* appear sensitive to UV-B (Zagarese et al. 1994; Zellmer 1998; Grad et al. 2001) and UV-A (320–400 nm) (Rautio and Korhola 2002*a*), showing decreased survival when exposed. *Daphnia* was the most UV-B-sensitive of several zooplankton taxa tested (Cywinska et al. 2000). Significant in-situ mortality was observed after 2 days of exposure at and above 73% of surface radiation at 320 nm but not at 63% (Zagarese et al. 1994). Survival of *Daphnia magna* was impaired after 4 and 8 h of exposure to UVR at DOM concentrations ≤1 mg C·L^{-1}, while 5 mg C·L^{-1} provided complete protection from 4 but not 8 h of exposure (Hessen and Faerøvig 2001).

There are several mitigating factors that may affect tolerance to UV-B, such as calcium level, pigment production, temperature, and behaviour. Hessen and Alstad Rukke (2000) found that low calcium concentrations can increase *Daphnia* sensitivity to UV-B. Declining calcium levels in some areas of eastern North America related to atmospheric deposition (Keller et al. 2001) may, therefore, complicate risk assessment. Some *Daphnia* produce melanin, a photoprotective pigment that absorbs UV-B (Hessen et al. 2002). Melanin concentration in subarctic lakes was a function of DOM concentration, increasing sharply below 3 mg C·L^{-1} (Rautio and Korhola 2002*b*). *Daphnia* were absent from subarctic ponds with DOM < 5 mg C·L^{-1}, and in ponds with DOM > 5 mg C·L^{-1}, melanin levels were higher than those in lakes with similar DOM concentrations, perhaps because deep-water refuges were not available. Elevated temperatures increased UV-B tolerance in *Daphnia catawba*; however, the temperature effect was species-specific (Williamson et al. 2002).

Daphnia migrate downwards to avoid UV-B (Leech and Williamson 2001), the extent of migration being an inverse function of pigmentation (Rhode et al. 2001). Less-pigmented animals could survive in clear waters provided that a deep-water refuge is available for shelter during daylight hours. The corollary of this is that *Daphnia* should be absent from clear waters without a refuge. Evidence supporting this supposition comes from a study of shallow ponds (<0.5 m depth) in Finnish Lapland (Rautio and Korhola 2002*b*). *Daphnia* were absent from ponds with DOM < 5 mg C·L^{-1}, perhaps because the ponds are too shallow to provide refuge from UV-B, although other factors associated with low DOM concentration, such as higher temperature (Rautio and Korhola 2002*a*) or increased visibility to predators, possibly have an effect.

Daphnia are very common and are often an important contributor to crustacean zooplankton biomass on the Canadian Shield (Yan et al. 1988). Loss of *Daphnia* would therefore lead to significant ecological changes. Based on their sensitivity to UV-B and their contribution to zooplankton biomass, *Daphnia* were explored as a potential biological indicator. On a cautionary note, the possibility exists that more UV-tolerant *Daphnia* species would supplant more sensitive daphnids; therefore, combining all *Daphnia* species may result in a loss of information.

Data on pH, *Daphnia* sp. abundance, Z_{max}, and DOM concentration from four surveys of lakes and ponds were pooled (Table 3). *Daphnia* spp. abundance data were available for 258 sites in Ontario and the northeastern USA in which DOM < 5 mg C·L^{-1} and maximum depth < 17 m. These sites were used to explore whether a relationship existed between *Daphnia* presence/absence and DOM concentration and Z_{max}.

DOM concentration was plotted against Z_{max} using symbols to indicate whether *Daphnia* were present or absent (Fig. 1). Acidic sites with pH < 5.3 were included because *Daphnia* have been observed in acidic lakes (Keller et al. 1992; Clair et al. 2001; N.D. Yan, unpublished data). For comparison, depths at which 1% of surface irradiance occurs for 320, 340, 360, and 380 nm and 10% for 320 nm are shown. If a lake or pond appears to the left of an extinction curve, say the 1% curve for 320 nm, then it is shallower than $Z_{320,1\%}$ and therefore irradiance at Z_{max} > 1%. Z_{max} in most lakes and ponds is below the depths that receive 1% and 10% of 320 nm. Only 14 acidic systems have small refuges or none at all, yet *Daphnia* are present in 5 of these. There is no strong evidence of any region in which *Daphnia* are excluded (Fig. 1). Hence, there does not appear to be a minimum level of DOM needed to protect *Daphnia* from extirpation, although systems with DOM < 1 mg C·L^{-1} and Z_{max} < 4 m are rare in the surveys. This implies that the effects of UV-B on distributions of other organisms will be difficult to detect unless they are much more sensitive to UV-B or are unable to escape to refuges.

Analysis of aquatic systems at risk in Canada based on DOM and Z_{max} distributions

In a worst case scenario, we assume that some taxa cannot tolerate even small amounts of UV-B at 320 nm (>1% of surface irradiance). Theoretically, these organisms should be excluded from systems in which $Z_{max} < Z_{320,1\%}$ and may be excluded from deeper systems if the refuge below $Z_{320,1\%}$ is unsuitable habitat. In this study, we consider a system to be optically clear if its DOM is such that irradiance at Z_{max} is

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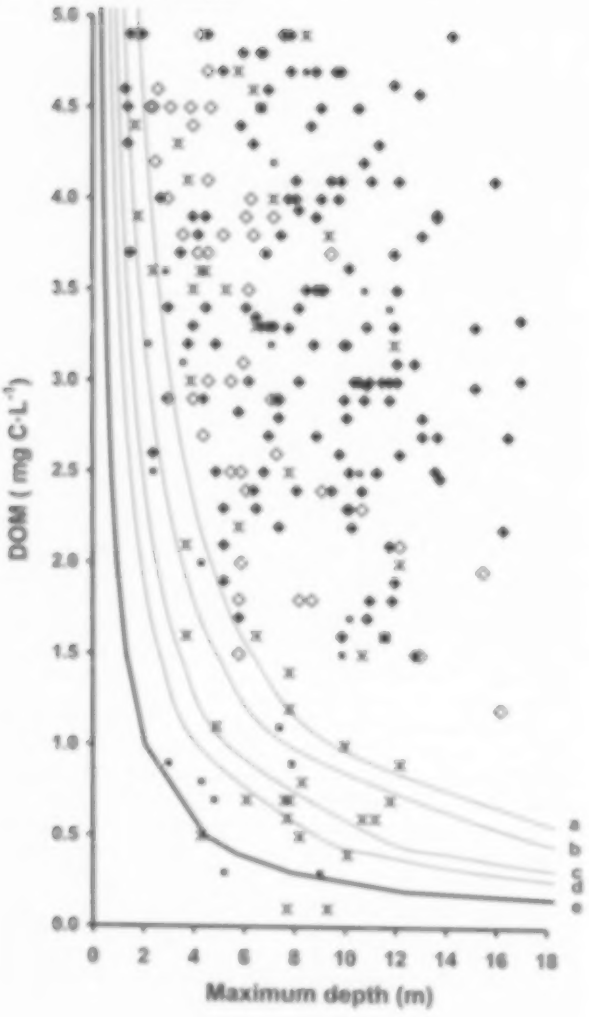
Fig. 1. Dissolved organic matter (DOM; mg C·L^{-1}) and maximum depth, Z_{max} (m), for 258 Ontario and US Environmental Monitoring Assessment Program Eastern Lake Survey sites. The broken lines are the depths at which 1% of surface irradiance at 320, 340, 360, and 380 nm occurs, assuming a particulate organic matter concentration of 0.4 mg C·L^{-1} (eqs. 5–8; see Table 2) (◇, Daphnia absent > pH 5.3; ◆, *Daphnia* present > pH 5.3; ×, *Daphnia* absent < pH 5.3; ■, *Daphnia* present < pH 5.3). Curves are as follows: $Z_{380,1\%}$ (*a*), $Z_{360,1\%}$ (*b*), $Z_{340,1\%}$ (*c*), $Z_{320,1\%}$ (*d*), and $Z_{320,10\%}$ (*e*). The curve for $Z_{320,1\%}$ is almost identical with the curve for $Z_{360,10\%}$.



greater than 1% of surface irradiance at 320 nm. Because shorter wavelengths have higher extinction coefficients, relative irradiance levels for wavelengths < 320 nm are less than 1% at $Z_{320,1\%}$. Hence, waters deeper than $Z_{320,1\%}$ are essentially UV-B-free. Also, $Z_{320,1\%}$ is very similar to $Z_{360,10\%}$, which means that waters above $Z_{320,1\%}$ will receive significant levels of UV-A > 360 nm. Note that atmospherically acidified lakes may still be clearer than their historical values in spite of recovery (Gunn et al. 2001).

Next, we define systems at risk as those that will become optically clear should they lose 50% of their DOM. However, DOM levels vary with time, and thus there is the danger that organisms in systems with low DOM concentrations may be temporarily exposed to UV-B. For example, the chromophoric portion of DOM can vary diurnally (Gibson et al. 2001) and seasonally (Clair et al. 1996; Morris and Hargreaves 1997; Laurion et al. 2000). The most plausible explanation is that as DOM ages it becomes more photobleached. This is consistent with the decline in colour–DOM ratios observed between headwater streams and lake outflows (Molot and Dillon 1997*a*).

Variation in allochthonous loading will affect DOM concentrations. Mean annual DOM varied <1 mg C·L^{-1} in three central Ontario lakes (regional runoff 0.4–0.6 m·year^{-1}) over a 12-year period from 1980 to 1992: 1.7–1.9 mg C·L^{-1} in Blue Chalk Lake, 3.9–4.6 mg C·L^{-1} in Crosson Lake, and 4.7–5.6 mg C·L^{-1} in Dickie Lake (P.J. Dillon, unpublished data). In any given year the maximum deviation from the long-term mean was between 7% and 11%. Thus, in a lake with a long-term mean DOM of 3.7 mg C·L^{-1}, the concentration may decline to 3.3 mg C·L^{-1} in some years, and in a lake with a long-term mean DOM of 1.7 mg C·L^{-1}, it might decline to 1.6 mg C·L^{-1} in some years. The DOM concentration varied more in other regions: in Lake 239 in northwestern Ontario (regional runoff 0.2 m·year^{-1}) (Schindler et al. 1997), DOM ranged from a high of about 8.6 mg C·L^{-1} in 1982 to a low of about 5.2 mg C·L^{-1} in 1984, a decline of 3.4 mg C·L^{-1} in 2 years. In Kejimkujik Lake in southwestern Nova Scotia (regional runoff 1 m·year^{-1}), DOM ranged from 3.0–13.0 mg C·L^{-1} with a mean of 6.9 mg C·L^{-1} between 1983 and 1999, although 91% of the samples were between 3 and 8.3 mg C·L^{-1} (Clair et al. 2001). Shallow systems can also exhibit large seasonal variation: in 11 of 13 wetland sites studied at St. Denis, Saskatchewan, DOM concentrations increased from spring to fall by an average of 64% (Waiser and Robarts 2004). Specific absorptivity in Prairie ponds decreases during the summer, even as DOM increases (Waiser and Robarts 2004).

In this study, a simplifying assumption is that temporal variation in chromophoric DOM concentration is relatively small in low-DOM systems (<5 mg C·L^{-1}), which are the primary systems of interest, while it is acknowledged that the risk analysis below might have to be revisited if this assumption proves to be dramatically violated. We also assume that regional variation in the chromophoric content of DOM is not significant in low-DOM systems. Data from Scully and Lean (1994) suggest that regional variation in chromophoric content is not large. However, other studies have shown that attenuation of UVR can vary regionally, in part because vegetation affects the chromophoric content of DOM. In the Tyrolian Alps in Europe, specific absorptivity at 320 nm was lowest among lakes with poor soil cover and highest among lakes with forest cover (Laurion et al. 2000). Regional differences in the chromophoric content of DOM are suggested by differences in specific UV-B attenuation (broadband UV-B attenuation coefficient (K_d)/DOM) between Prairie and non-Prairie freshwater lakes (Scully and Lean 1994; Arts et al. 2000). However, specific UV-B attenuation in non-Prairie lakes sampled by Scully and Lean (1994) is similar to that in Prairie ponds (Arts et al. 2000).

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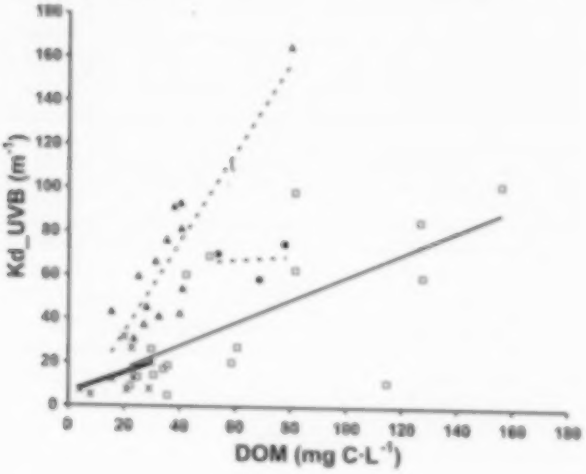
Fig. 2. Ultraviolet B (UV-B) attenuation coefficients (K_d) versus DOM in Saskatchewan lakes and ponds (data from Arts et al. 2000) (°, non-saline lakes; □, saline lakes; ▲, non-saline ponds; ●, saline ponds).



Saline systems are quite different from freshwater systems (Fig. 2) (Arts et al. 2000; Waiser and Robarts 2000). Most prairie saline systems have much lower specific attenuation than freshwater systems and high DOM concentrations (>20 mg C·L^{-1}) (Fig. 2). None of the 3 saline ponds and only 2 of the 17 saline lakes surveyed by Arts et al. (2000) in Saskatchewan had a K_d value < 10 m^{-1}, which is the maximum value in the freshwater, low-DOM lakes (<5 mg C·L^{-1}) measured by Scully and Lean (1994). Although saline ponds have lower specific absorptivity and thus a higher proportion of non-chromophoric DOM (Arts et al. 2000; Waiser and Robarts 2000), their much higher DOM levels result in significant UV-B attenuation.

We operationally define systems at risk here as systems that are not now optically clear but in which loss of 50% of DOM would result in $Z_{320,1\%} \geq Z_{max}$. We are now in a position to estimate the number of systems in ecozones across Canada that are naturally optically clear or at risk of becoming optically clear should DOM decrease.

Data were collected from all 15 ecozones across Canada (Table 4). The number of sites with complete data varied dramatically from 5 in the Taiga Plains ecozone to over 500 in the Boreal Shield ecozone. All ecozones are represented by at least 24 sites except the Taiga Cordillera (5) and Taiga Plains (6). Results from the latter two ecozones should therefore be treated with caution.

Median DOM concentrations varied dramatically among ecozones, ranging from 1.1 mg C·L^{-1} on Victoria Island in the Northern Arctic to 14.7 mg C·L^{-1} in the Boreal Cordillera, with the exception of the Prairies (Table 4). Median Prairie non-saline and saline concentrations were 39 and 59.8 mg C·L^{-1} in Saskatchewan and 46 and 120 mg C·L^{-1} in Alberta, respectively.

The proportion of systems currently deemed optically clear is quite low (<6%) in most regions south of the treeline, with 10%–20% in the Montane Cordillera (Kamloops, Prince George, and Continental Divide regions) and Pacific Maritime ecozones (Table 4). Optically clear ponds are more common in the Hudson Plains and Southern Arctic ecozones (0%–13%) and are the norm in the Northern Arctic and Northern Cordillera ecozones (31%–100%). Community structure in these clear systems may, perhaps, reflect the effects of UV-B exposure. If, however, a sensitive aquatic biota was able to tolerate, say, no more than 10% of surface radiation at 320 nm rather than 1%, then the proportion of optically clear systems would be smaller.

The proportion of systems deemed to be at risk was 0% in most regions south of the treeline and between 5% and 9% in the Boreal Shield (Ontario and Newfoundland), Atlantic Maritime (Nova Scotia), and Montane Cordillera ecozones along the Continental Divide (Table 4). The proportion of ponds at risk ranged from 0% to 28% in the Southern Arctic and from 11% to 62% in the Northern Arctic. No systems at risk occurred at Cape Herschel on Ellesmere Island in the Arctic Cordillera because all ponds were optically clear. These estimates are based on a worst case scenario in which it is assumed that there exist very sensitive organisms incapable of tolerating more than 1% of surface irradiance at 320 nm. If these sensitive organisms are able to tolerate up to, say, 10% of surface irradiance at 320 nm, then the proportion of systems at risk (*i.e.*, systems without refuge below $Z_{320,10\%}$) would be smaller.

There is a note of caution regarding wetlands: many of these shallow systems can lose considerable water volume and therefore depth as a result of strong evaporation. Consequently, deeper water refuges from harmful UV-B may disappear with relatively low DOM concentration, especially in very dry years.

DOM < 5 mg C·L^{-1} in a large fraction of systems on the Boreal Shield in Ontario (53% and 39% in the OMOE and CWS surveys, respectively). Because depth data are not available, we take these estimates to represent the upper bounds for the proportion of systems at risk. The actual proportion is likely much less, as indicated by the small proportions of Boreal Shield systems at risk in the Algoma, Sudbury, and Muskoka–Haliburton regions of Ontario, the Abitibi region of Quebec, and Newfoundland (5%, 0%, and 6%, respectively).

Discussion and conclusions

This study suggests that DOM levels are adequate to prevent large-scale loss of *Daphnia* and perhaps other similarly sensitive taxa from direct exposure to UV-B at current incident levels in most regions below the treeline in Canada. In contrast, a large proportion of ponds in the Canadian Arctic are either optically clear or at risk. These conclusions are based on two approaches: (1) a comparison of Z_{max} with $Z_{320,1\%}$ in conjunction with the presence/absence of *Daphnia*, and (2) biogeochemical estimates of the numbers of "optically clear" and "at-risk" systems across Canada. Although we tentatively conclude that UV-B-induced extirpation of *Daphnia* and similarly sensitive taxa is probably not a major concern south of the treeline, even if a 50% loss of DOM should occur, generalizing this to conclude that loss of DOM will not affect species richness requires that (*i*) additional chemical and morphometric data be collected, especially from shallow ponds south of the treeline, and (*ii*) additional sensitive taxa be identified to which a

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Table 4. Percentages of surveyed lakes and ponds that are optically clear and at risk in Canadian ecozones.

	N	Median DOM (mg C·L^{-1})	Clear (%)	At risk (%)
Atlantic Maritime				
Nova Scotia[a]	45	5.8	4	7
New Brunswick	11	3.4	0	0
Mixedwood Plains	33	6.1	0	0
Boreal Shield				
Ontario[b]	2744	4.7		53[c]
Ontario[b]	4488	5.8		39[c]
Ontario[d]	499	3.7	6	5
Quebec	42	8.7	e	e
Newfoundland[a]	16	4.3	0	6
Prairies				
Saline[f,f]	20	59.8	0	0
Saline[g]	17	120	0	0
Non-saline[f]	24	39	0	0
Non-saline[g,h]	8	46	0	0
Boreal Plains				
Alberta[f]	1	18	e	e
Wood Buffalo Park[i]	30	36.0	0	0
	5	3.6		
Taiga Plains[b]	5	13.1	0	0
Taiga Shield	11[k]	5.7	0	0
	38	24.5	0	0
Montane Cordillera	66[l]	1.5	14	9
	61[k]	12.3	10	0
	50[l]	11.4	0	0
Pacific Maritime[m]	60	3.2	20	0
Boreal Cordillera[b]	24	14.7	e	e
Taiga Cordillera[b]	6	8.3	0	0
Hudson Plains[n]	38	9.4, 13.0	13	8
Southern Arctic	37[k]	6.3	0	0
	18	2.3	6	28
Northern Arctic[o]				
Axel Heiberg Island				
Ponds	26	3.9	89	11
Lakes	12	2.3		
Victoria Island				
Ponds	28	1.5	100	
Lakes	6	1.1		
Banks Island				
Ponds	32	7.0	52	33
Lakes	9	3.4		
Prince Patrick Island, Mould Bay				
Ponds	32	6.9	31	62
Lake	1	3.5		
Arctic Cordillera[o]				
Ellesmere Island, Cape Herschel, ponds	37	4	100	0

Note: A clear lake is one with a DOM concentration such that irradiance at maximum depth, Z_{max}, > 1% of surface irradiance at 320 nm. A lake is at risk if it is not now optically clear but would become so upon losing 50% of its DOM. *N* is the total number of surveyed systems.

[a]Multiyear means.

[b]Some lakes are duplicated in the Canadian Wildlife Service (CWS) and Ontario Ministry of Environment surveys. Maximum depths are not available.

[c]Percentage of all lakes with DOM < 5 mg C·L^{-1} because maximum depths are not recorded.

[d]Data from CWS, Yan, and Keller zooplankton surveys (see Table 3).

[e]The lowest DOM concentration in saline lakes and ponds is 22.1 mg C·L^{-1}. In a non-saline lake, DOM of 12.2 mg C·L^{-1} would provide similar UV-B attenuation.

[f]Sites from Saskatchewan. Maximum depths are not available. However, depths at which 1% UV-B penetration occurs are much less than probable maximum depths (<90 cm in lakes and <15 cm in ponds), implying that refuges exist and systems are not at risk from UV-B.

[g]Sites from Alberta. Mean depths ranged from <1 to 2.5 m. Includes saline and moderately saline systems.

[h]Maximum depth estimated as Z_{max} = 2.88 × mean depth + 0.60, R^2 = 0.82. The regression was derived from data for 33 Ontario lakes (Molot et al. 1992).

[i]DOM concentrations are means. Thirty lakes are classified as muskeg and sinkhole and 5 lakes as Canadian Shield lakes. Depths are not reported (Moser et al. 1998).

[j]All lakes from the Continental Divide region.

[k]All lakes from the Prince George and Kamloops regions.

[l]Most sites are north of Prince George within approximately 300 km. Three of the northeastern lakes may be in the Boreal Plains ecozone (Bos and Cumming 2003).

[m]Of the 60 lakes, 56 are on Vancouver Island.

[n]Mean depths measured in 37 of 38 ponds were <0.6 m on 19 June 1995. DOM ranged from 4.8 to 42.6 mg C·L^{-1} on 19 June 1995 and 13 August 1997, respectively. Maximum depth is estimated as 2.88 × Z_{max} + 0.60.

[o]Proportions based only on those systems where approximate depth is recorded.

presence/absence analysis can be applied. Moreover, this study does not address the possibility that UV-B affects systems in subtler ways than extirpation. Exploration of the extent of subtle effects will require experimental identification and then widespread measurement of appropriate indicators across Canada.

An assessment of 136 ponds and small lakes in the US Pacific Northwest suggested that DOM levels are sufficient to protect developing amphibian eggs from UV-B in 85% of the sites (Palen et al. 2002). Similarly, an assessment of wetlands in northern Minnesota (a region similar to the Boreal Shield ecozone) also showed that DOM provided adequate protection to the northern leopard frog, *Rana pipiens*, in most wetlands (Ankley et al. 2002; Diamond et al. 2002; Peterson et al. 2002). The latter assessment was based on experimentally determined dose–response relationships for developing eggs (removed from their egg masses) and tadpoles. While experimental exposure to full sunlight reduced tadpole survival and caused malformation of tadpoles, the modeling component showed that DOM provided sufficient protection in 21 of 26 wetlands, assuming a worst case scenario (that tadpoles remain within the top 10 cm of the water column). However, tadpoles probably reduce their exposure to UV-B by spending part of the day in the shade or hiding under natural objects in situ rather than remaining within the top 10 cm of the water column (as per the experimental protocol). Even very clear ponds have refuges, at least in forested areas, and thus may support frog populations. Furthermore, in a review of studies of the effects of UV-B on developing amphibian eggs, Licht (2003) found possible negative effects for 9 species and no significant effects for 25 species. Three of the 31 species tested exhibited either possible effects or no significant effects, depending on the study. Licht (2003) also argued that experimental proto-

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cols can sometimes generate unrealistic conditions. Therefore, the percentage of wetlands in the US Pacific Northwest and northern Minnesota that provide adequate protection to developing amphibians is probably underestimated.

This study did not assess the extent to which DOM may decrease. Significant regional variation in response to climate change is predicted by the Canadian General Circulation Model, especially north of the treeline and on the Prairies (Canadian Centre for Climate Modelling and Analysis 2003). Hence, the probability of experiencing decreasing DOM and increasing exposure is not constant among ecozones. In general, DOM export from catchments to surface waters will decrease if there is a reduction in peatland area (Dillon and Molot 1997). This, in turn, may occur if there is a significant long-term reduction in runoff.

We express a word of caution at a time when the search for sentinel indicators of ecosystem health is in full swing: our study suggests that obtaining experimental evidence of sensitivity of organisms to a stressor should not lead us to automatically conclude that these organisms are effective indicators or that significant ecological impacts will occur in nature. Instead, the existence of experimental evidence should lead us to hypothesize that an organism is affected in situ, and then to test this hypothesis as we did here. In some cases, an organism's unexpected resilience in situ may mean that behaviours or characteristics that provide protection have been overlooked in experimental studies.

There are two issues worth mentioning. (1) This study defined risk incurred through increased UV-B exposure only in terms of loss of DOM. If risk is to be more fully defined by loss of DOM, then a suite of indicators should be expanded to include other impacts associated with loss of DOM, such as changes in heating and visible-light penetration to name just two. Loss of DOM would lead to a larger, clearer epilimnion and smaller hypolimnion in lakes deep enough to stratify (Gunn et al. 2001). An empirical formula recently developed to predict optimal lake trout (*Salvelinus namaycush*) habitat in Ontario (Dillon et al. 2003) predicts that a decline in DOM from 8 to 7 mg C·L^{-1} would result in the depth at which 10 °C occurs at the end of the summer ($Z_{10\ °C}$) becoming 0.2 m deeper but a decline from 3 to 2 mg C·L^{-1} would result in $Z_{10\ °C}$ becoming 1.9 m deeper. As is the case with UV-B, systems with relatively low DOM are more at risk of heating from loss of DOM (Gunn et al. 2001), and as we have shown here, most ecozones outside the Prairies have large numbers of low-DOM (<3 mg C·L^{-1}) systems. (2) Owing to variation in the proportions of chromophoric and non-chromophoric DOM, we recommend that future surveys also measure underwater radiation transmission in addition to DOM. Because direct measurement of in-situ irradiance requires expensive equipment not available in many laboratories, we recommend instead measuring absorbance of unfiltered surface samples throughout the UVR and visible regions (a path length > 1 cm will be needed for longer wavelengths and clear waters).

Although there are no guidelines for judging what percent loss is acceptable, current critical load targets for acid deposition in North America provide a model. Critical load targets are based on the desirability of maintaining 95% of lakes in each deposition region above the critical pH threshold of 6; that is, 5% of lakes will not be protected (Jeffries 1997). Using this criterion, DOM levels in most regions south of the treeline appear to be adequate to protect aquatic systems from significant species losses, with the possible exception of 5%–9% of systems in Nova Scotia and Newfoundland and along the Continental Divide. However, DOM levels are probably not adequate to protect 95% of systems north of the treeline.

This should not be construed to suggest that UV research is no longer necessary. In fact, there is a consensus that less dramatic UVR-mediated impacts are quite important. For example, UV-A induces photorepair (Quesada et al. 1995) and may inhibit photosynthesis (Callieri et al. 2001). UV-A is also responsible for the majority of photooxidative loss of DOM (Molot and Dillon 1997*b*). Our understanding of these roles is only emerging, therefore process-based ecological research on both UV-B and UV-A should continue. Future research may shape our understanding of how aquatic organisms have evolved to cope with UVR and the extent to which subtler impacts occur.

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ERRATUM / ERRATUM

Erratum: Effect of the North Atlantic Oscillation on recruitment of Atlantic cod (*Gadus morhua*)

K. Brander and R. Mohn

Ref.: Can. J. Fish. Aquat. Sci. **61**: 1558–1564 (2004).

The first "exp" appearing in eqs. 2 and 3 should have been "exp(1)". The correct equations are as follows:

(2) $$R = \exp(1) \times (R_{max}/SSB_{max}) \times SSB \times \exp(-SSB/SSB_{max})$$

(3) $$R = \exp(1) \times (R_{max}/SSB_{max}) \times SSB \times \exp(-SSB/SSB_{max}) \times \exp(c \times NAO)$$

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K. Brander.[1] International Council for the Exploration of the Sea, Palægade 2-4, 1261 Copenhagen K, Denmark.
R. Mohn. Marine Fish Division, Bedford Institute of Oceanography, Fisheries and Oceans Canada, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada.

[1]Corresponding author (e-mail: keith@ices.dk).

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Canadian Journal of Fisheries and Aquatic Sciences

Author Index
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Index des auteurs
Volume 61, 2004

Abrams, P.A., 175
Adamson, M.L., 1143
Agnew, D.J., 1048
Agostini, V.N., 360
Ajiad, A.M., 1900
Albanese, B., 857
Albert, D., 1113
Alfredsson, Á., 230
Allen, J.I., 765
Alò, D., 1890
Alonso, M.K., 1681
Amiro, P.G., 1965
Amsinck, S.L., 1988
Andersen, N.G., 2413
Anderson, C.S., 168
Anderson, M.J., 1294
Anderson, N.J., 1988
Andrews, A.H., 443
Anesio, A.M., 1520
Angermeier, P.L., 857
Antunes, J.C., 432
Appleby, P.G., 1988
Archer, S.D., 765
Arkhipkin, A.I., 1212
Arkoosh, M.R., 1166
Armstrong, J.D., 2401
Armstrong, T.W., 2025
Árnason, A., 230
Arts, M.T., 2511
Ashworth, A.C., 1807
Aumont, O., 826
Bacon, C.R., 2425
Bacon, P.J., 2278
Bajer, P.G., 2158, 2168
Baldwin, D.H., 404
Barber, I., 1832
Barbiero, R.P., 2111
Barko, J.W., 538
Baron, J.S., 1153, 1256
Barton, D.R., 1285
Bartsch, L.A., 1102
Batzer, D.P., 529
Bazzi, A., 1871
Beddington, J.R., 1048
Beechie, T.J., 590
Beland, K.F., 2392
Bello, R., 2511
Bellows, W.K., 685
Belviso, S., 804, 826
Bennett, W.A., 2499
Bentzen, P., 193
Berg, O.K., 2151
Bergeron, N.E., 2271
Berk, L., 1124
Berkeley, A., 487
Bernier, N.J., 1797
Berry, C.R., Jr., 954
Bérubé, F., 2271
Bilby, R.E., 999
Biro, P.A., 1513
Bishop, G., 1404
Blackford, J., 765
Blausey, C.M., 954
Block, B.A., 1976
Boeuf, G., 1247
Bogstad, B., 343
Boisclair, D., 2267, 2302
Booth, B., 2038
Bopp, L., 804, 826
Borelli, G., 1247
Borges, L., 1918
Bosley, K.L., 2069
Bøthun, G., 870
Botsford, L.W., 1325
Bouça, P.D., 432
Bouchard, P., 1225
Boucher, O., 826
Boutillier, J., 1404
Boutillier, J.A., 1373, 2126
Brander, K., 1558, 2522
Brauner, C.J., 1797
Brauner, J.B., 999
Briand, G., 43
Briffa, M., 1627
Brown, T.A., 443
Buchanan, C.K., 887
Buffington, J.M., 2085
Bujold, V., 273
Buzby, K.M., 1954
Caddy, J.F., 1307
Cadrin, S.X., 1373
Cailliet, G.M., 443
Campana, S.E., 1212, 1269
Campbell, A., 1325
Campbell, P.G.C., 1702
Cantin, G., 744
Carder, D.A., 1124
Cardinale, M., 158
Castonguay, M., 2194
Castro-Santos, T., 1590, 1602
Cavanaugh, J.C., 1102
Chabot, D., 2194
Chambers, R.C., 2069
Charlton, M.N., 1285
Chen, Y., 122, 134
Chernyak, S.M., 627
Choat, J.H., 323
Choi, J.S., 505
Chow-Fraser, P., 1113
Christensen, I., 230
Clair, T.A., 1965, 2511
Clark, W.G., 1881
Clarke, A.L., 1988
Clerk, S., 1691
Coale, K.H., 443
Coimbra, J., 432
Collier, T.K., 1166
Colt, J., 511
Congleton, J.L., 1066
Cook, E.A., 1503
Cope, J.M., 332
Cordell, J.R., 1
Cosby, B.J., 1965
Coulombe-Pontbriand, M., 648
Courtemanche, D.A., 273
Couture, P., 942
Cox, S.P., 1658
Crespo, E.A., 1681
Creuzé des Châtelliers, M., 1817
Crook, D.A., 2183
Cumming, B.F., 986
Cunjak, R.A., 273, 1717
Curtis, P.J., 2511
Cury, P., 414
Dacey, J.W.H., 758, 788, 836

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Dolsgaard, J., 1671
Dananchet, D., 476
Dans, S.L., 1681
Dauble, D.D., 23
Davies, J.-M., 1538
Davis, A., 1191
Deegan, L.A., 1954
Deibel, D., 1940
Dempson, J.B., 2384
Dennis, I.F., 1965
De Pontual, H., 1247
Despatie, S.-P., 2194
Dettmers, J.M., 12
Dick, J.T.A., 1627
Dietrich, J.P., 273
Dillon, P.J., 2511
DiTullio, G.R., 721
Dodson, J.J., 54
Doering-Arjes, P., 158
Dorai-Raj, S., 857
Dorn, N.J., 2135
Douglas, M.S.V., 1235, 2511
Dowling, N.A., 247, 260
Downing, J.A., 1784
Drinkwater, K., 505
Dubreuil, T., 2288
Dufresne, J.-L., 826
Dulvy, N.K., 466
Dunn, A.M., 1627
Eakin, H.L., 538
Edeyer, A., 1247
Edward, A., 758
Egertson, C.J., 1784
Enders, E.C., 2302
Engstrom, D.R., 561
Erkinaro, J., 2329, 2384
Essington, T.E., 2215
Etnier, M.A., 1616
Eveson, J.P., 292, 307
Farrell, A.P., 1225
Feist, B.E., 999
Feng, C.C., 1447
Feng, J.C., 1447
Feng, P., 1124
Fielding, N.J., 1627
Finneran, J.J., 1124
Finney, B.P., 1235
Finstad, A.G., 2151, 2358
FitzGerald, J., 1212
Fitzpatrick, J.A., 2425
Fivelstad, S., 511
Flynn, L., 80
Fogarty, M.J., 1392
Forseth, T., 2358
Francis, R.C., 360
Francis, R.I.C.C., 1269
Frank, K.T., 505
Frantz, B.R., 443
Friedl, D., 2144
Fritz, S.C., 561
Fukuchi, M., 736
Gallardo, J.A., 547
Gammelgaard, M., 2038
García, X., 547
Gaudin, P., 476
Gauthier, S., 1839
Geist, D.R., 23
Gendron, L., 1392
Gephard, S., 2392
Gerdeaux, D., 1485
Gérimo, M., 1817
Gessner, M.O., 2007
Gibson, A.J.F., 1771
Giguère, A., 1702
Gilbert, F.J., 765
Girard, I.L., 2339
Godø, O.R., 2237
Goetz, F.A., 1756
Gosselin, M., 712, 744
Graham, N.A.J., 466
Granéli, W., 1520
Grant, G.C., 168
Grant, J.W.A., 2339
Graves, J.A., 1176
Gray, M.A., 1717
Greenberg, H.M., 2085
Greene, C.M., 590
Gregory-Eaves, I., 1235, 2440
Grenouillet, G., 93
Griswold, K., 2288
Guderley, H., 1225
Guildford, S.J., 1285
Gusev, E., 1900
Gust, N., 205, 323
Haeseker, S.L., 2471
Haggerty, S.M., 529
Hajas, W., 2126
Häkkinen, P.J., 1520
Hall, K.J., 384
Hall, N.G., 1202
Hall, S.J., 247, 260
Hammar, T., 2014
Hammill, M.O., 2194
Hammond, T.R., 1647
Hand, C.M., 1355
Handeland, S., 511
Hannah, R.W., 487
Hanrahan, T.P., 23
Hanson, J.M., 1191
Hansson, S., 2215
Harada, H., 700
Hardie, D.C., 1636
Hare, L., 1702
Haro, A., 1590
Hassinen, E., 2384
Hatcher, M.J., 1627
Hattala, K.A., 924
Hawes, E.J., 2350
Hayward, R.S., 2158, 2168
Heard, S.B., 887
Heath, J.W., 1797
Hebert, P.D.N., 1636
Heckelei, T., 43
Hecky, R.E., 1285
Heikkola, E., 2227
Heneman, B., 2499
Hérissé, C., 93
Herwig, B.R., 12
Hesp, S.A., 1202
Hicks, W.A., 758
Hilborn, R., 80, 1355
Hill, A.M., 2255
Hill, R.W., 758
Hill, S.D., 758
Hill, S.L., 1048
Hillman, G.R., 1447
Hinch, S.G., 905
Hintsa, E.J., 836
Hjellvik, V., 2237
Hjermann, D.Ø., 1747
Hodges, A.L., 323
Holm, M., 2384
Holt, C.A., 2455
Horne, J.K., 1839
Horppila, J., 1862
Hovgård, H., 636
Howell, T., 1285
Hrafnkelsson, B., 1135
Hudon, C., 603
Hughes, N.F., 103
Hüssy, K., 1012, 1021
Huusko, A., 185, 2329
Idoine, J.S., 1373
Ingvaldsen, R., 2384
Jackson, C.R., 529
Jacobson, P.C., 2144
James, W.F., 538
Jarvi, T., 328
Jenkins, J.J., 404
Jenks, J.A., 954
Jensen, D.W., 999
Jeppesen, E., 1988
Jessen, F., 1012
Jiao, Y., 122, 134
Johansen, G.O., 343

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Johnson, B.M., 1153, 1256
Johnson, L., 1166
Johnson, R.K., 1493
Johnson, S.L., 913
Johnston, N.T., 384
Johnston, P., 2271
Johnston, T.A., 110
Jones, C.M., 34
Jones, J.R., 1503
Jones, N.E., 1736
Jonsson, B., 2369
Jonsson, N., 2369
Juanes, F., 2392
Julkunen, M., 2384
Jurvelius, J., 2227
Kahnle, A.W., 924
Kalinowski, S.T., 1075
Kasamatsu, N., 736
Kastowsky, M., 158
Kaufman, L., 2499
Kaufmann, P.R., 283
Kawaguchi, S., 736
Keller, M.D., 685
Keller, W., 2511
Kelly, C., 1124
Keogh, M.J., 1124
Kerr, L.A., 443
Kiene, R.P., 685, 700
Kiessling, A., 452
Kiessling, K.-H., 452
Kincaid, T.M., 283
King, S.E., 487
Kingsford, M.J., 898
Kirkwood, G.P., 1048
Kjeld, M., 230
Klitzke, J., 2144
Knapp, R.A., 2025
Knowlton, M.F., 1503
Kopplin, C.J., 954
Kostow, K.E., 577
Kratz, T.K., 2255
Kroglund, F., 511
Labonne, J., 476
Ladwig, A., 147
Lafrançois, B.M., 1153, 1256
Laird, K.R., 986
Landkildehus, F., 1988
Lankester, M.W., 1143
Lapointe, M., 648
Lapointe, M.F., 2271
Laroche, D., 744
Larsen, D.P., 283
Larsen, K.A., 2425
Laslett, G.M., 292, 307
Lawson, P.W., 360
Leavitt, P.R., 2511
Le Clainche, Y., 788
Leggett, W.C., 110, 505
Lehman, J.T., 1871
Lenormand, S., 54
Lessa, E.P., 1095
Letcher, B.H., 2288, 2314
Levasseur, M., 712, 744, 788
Levings, C.D., 1
Lewy, P., 636, 2487
Lhorente, J.P., 547
Lilja, J., 2227
Liljendahl-Nurminen, A., 1862
Lindahl-Kiessling, K., 452
Litvin, S.Y., 1851
Lobón-Cerviá, J., 1929
Lodge, D.M., 2255
Logerwell, E.A., 360
Lovejoy, C., 2038
Lundquist, H., 328
Macdonald, J.S., 1225
MacIsaac, E.A., 384
MacNeil, C., 1627
MacPherson, H., 1191
Macrae, M., 2511
Madenjian, C.P., 627
Magnuson, J.J., 2255
Mäki-Petäys, A., 2329
Malcolm, I.A., 2278
Malinen, T., 1862
Mantua, N.J., 360
Marjomäki, T.J., 2227
Marshall, C.T., 1900
Martin, G.B., 34
Martin, J., 110
Matrai, P.M., 685
Matsuda, H., 175
Matteson, K.M., 487
Matulich, S.C., 43
Mayer-Gostan, N., 1247
Mazumder, A., 1538
McAllister, M.K., 1032, 1048
McArdle, B.H., 1294
McCulloch, M.T., 898
McDonald, D.G., 618, 942, 1702
McGarvey, R., 247, 260
McKelvey, S., 2401
McNicol, D.K., 2511
Mehl, S., 343
Ménard, A., 54
Mermillod-Blondin, F., 1817
Merz, J.E., 1433
Merzouk, A., 712
Meyer, E.I., 1565
Michaud, S., 712, 744
Michielsens, C.G.J., 1032
Mill, A.C., 466
Miller, J.A., 1723
Miller, R., 1325
Miscampbell, A.E., 1143
Mittelbach, G.G., 2135
Mittlehammer, R.C., 43
Mohn, R., 1558, 2522
Molot, L.A., 2511
Monfray, P., 826
Monroe, E.M., 1102
Montgomery, D.R., 2085
Moore, J.W., 1582
Morissette, L., 2194
Morton, A., 147
Morton, A.E., 1513
Mosegaard, H., 158, 1012, 1021
Mostajir, B., 2038
Moulin, C., 804
Munday, P.L., 323
Munkittrick, K.R., 1717
Muotka, T., 2329
Myers, R.A., 1771
Næsje, T.F., 2358
Needle, C.L., 1900
Neil, S.R.E., 2097
Neira, R., 547
Nelson, R., 2144
Newbrey, M.G., 1807
Nielsen, J.R., 636
Niemelä, E., 2329, 2384
Nightingale, P.D., 765
Nislow, K.H., 2288, 2401
Niyogi, S., 942
Nordin, R.N., 2511
Noreika, J., 1590
Nosher, T., 1871
Nowlin, W.H., 1538
Nriagu, J.O., 1871
Nydick, K.R., 1153, 1256
Nykänen, M., 185
Obedzinski, M., 2288, 2314
Obrecht, D.V., 1503
O'Connell, V., 1083
O'Connor, D.V., 627
Odate, T., 736
Odeh, M., 1590
O'Donnell, M.J., 2288
O'Dor, R.K., 1976
Officer, R., 1918
Øien, N., 870
Ojaveer, E., 219
O'Keefe, J.P., 627
Ólafsson, Ö., 230
Olsen, A.B., 511

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Olsén, K.H., 328
Ong, S., 1
Orensanz, J.M., 1355
Ostrofsky, M.L., 1493
Ottersen, G., 1747
Parker, S.J., 487
Parkinson, E.A., 1513, 1658
Parma, A.M., 1355
Parrish, C.C., 1940
Parrish, D.L., 2350
Pascual, M.A., 1095
Pasternack, G.B., 1433
Patterson, D.A., 1225
Patterson, H.M., 898
Payan, P., 1247
Pedraza, S.N., 1681
Peet, C., 147
Pepin, P., 659
Perga, M.-E., 1485
Perry, W.L., 2255
Pess, G.R., 999
Peterman, R.M., 2455, 2471
Petersson, E., 328
Pham, M., 826
Phillips, A., 2126
Pienitz, R., 2440, 2511
Piercey, G.E., 1
Pitcher, T., 374
Poeppperl, R., 1565
Polacheck, T., 292, 307
Polunin, N.V.C., 466
Pont, D., 93
Post, J.R., 1513, 1658
Potter, I.C., 1202
Pouliot, M.-A., 2271
Pradel, R., 476
Prairie, Y.T., 2440, 2511
Prenter, J., 1627
Prusov, S., 2384
Purcell, S., 519
Pyle, G., 942
Quinn, T.J., II, 974
Quinn, T.P., 193
Racca, J.M.J., 2440
Radomski, P., 168
Ragnarsson, B., 328
Rago, P., 1338
Rahel, F.J., 1528
Raid, T., 219
Raikow, D.F., 497
Ralston, S., 1083
Ramstack, J.M., 561
Rand, P.S., 905
Randall, D.J., 1797
Rasmussen, J.B., 1702
Rediske, R.R., 627
Regnell, O., 2014
Reisenbichler, R., 2425
Reynolds, J.E., III, 554
Richardson, W.B., 1102
Richoux, N.B., 1940
Riddell, G.E., 1627
Riis-Vestergaard, J., 2413
Rindorf, A., 2487
Riseman, S.F., 721
Ritchie, M.G., 1176
Riva Rossi, C.M., 1095
Robarts, R.D., 2511
Roberts, C.M., 2053
Rodwell, L.D., 2053
Rogan, E., 1918
Rogers-Bennett, L., 2499
Roinestad, K., 2499
Romano, T.A., 1124
Rönkkönen, S., 219
Rose, G.A., 1553
Rossi, T., 2227
Rossignol, P.A., 1166
Rouse, M.-A., 700
Routledge, R., 147
Roy, A.G., 2302
Roy, S., 744, 2038
Ruggerone, G.T., 1756
Ryves, D.B., 1988
Sainte-Marie, B., 1303, 1404
Salas, S., 374
Sandahl, J.F., 404
Saucier, F.J., 788
Sauvage, S., 1817
Savenkoff, C., 2194
Savereide, J.W., 974
Scarratt, M., 712, 744
Schindler, D.E., 1582
Schindler, D.W., 1461
Schlundt, C.E., 1124
Schneider, D., 122, 134
Scholz, N.L., 404
Schrank, A.J., 1528
Schweder, T., 870
Scott, G.R., 618
Seamons, T.R., 193
Seitz, A., 1976
Selbie, D.T., 1691
Setka, J.D., 1433
Shanks, A.L., 1723
Sheer, M.B., 999
Shin, Y.-J., 414
Siddeek, M.S.M., 1404
Sigler, M.F., 1475
Simó, R., 673
Skaug, H.J., 870
Sloman, K.A., 618
Smith, R.E.H., 1285
Smith, S.J., 1303, 1338
Smol, J.P., 1235, 1691, 2511
Soballe, D.M., 1102
Soluk, D.A., 12
Soulsby, C., 2278
Spänhoff, B., 2007
Standen, E.M., 905
Starr, R.M., 1083
Steel, E.A., 999
Stefánsson, G., 1135
Stefansson, S., 511
Stefels, J., 804
Steingrímsson, S.Ó., 2339
Stenseth, N.C., 1747
St. John, M., 1671
Stokesbury, M.J.W., 1976
Stoner, A.W., 238
Strauss, E.A., 1102
Strayer, D.L., 924
Stuen, S., 230
Sturm, E.A., 238
Su, Z., 2471
Sumaila, U.R., 374
Sunda, W., 700
Svenning, M.A., 2384
Tank, S.E., 1461
Taylor, E.B., 68
Taylor, W.D., 1285
Teo, S.L.H., 1976
Thompson, R.J., 1940
Thomsen, H.A., 2038
Thorley, J.L., 2278
Thorrold, S.R., 34, 1212
Tjøstheim, D., 2237
Todd, C.D., 1176
Tonn, W.M., 1736
Tremblay, J.-E., 2038
Trippel, E.A., 2097
Tryland, M., 230
Tschaplinski, P.J., 384
Tuchman, M.L., 2111
Turner, T.F., 1890
Ugedal, O., 2358
Ulltang, Ø., 343
Urquhart, N.S., 283
Uthicke, S., 519
Valero, J., 1355
Verschuren, D., 986
Vézina, A., 744, 788
Vézina, A.F., 845, 2194
Vidussi, F., 2038
Viitasalo, M., 219

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Vingum, L., 1102
Vollenweider, J.J., 1475
Waagbø, R., 511
Wadleigh, M.A., 817
Wagner, T., 1066
Wahl, D.H., 12
Wainright, S.C., 2069
Waiser, M.J., 2511
Walker, A.F., 1176
Walker, A.M., 1176
Wall, S.S., 954
Walters, C., 1061
Wang, Y., 1447
Wares, J.P., 1890
Watanabe, S., 736
Watts, H., 1191
Weber, P.K., 2425
Wei, A., 1113
Weinstein, M.P., 1851
Wetzel, D.L., 554
Whalen, K.G., 2350
Wheaton, J.M., 1433
Whitledge, G.W., 2158, 2168
Wiegand, M.D., 110
Willis, T.V., 2255
Wilson, J.M., 432
Wilson, K.A., 2255
Wilson-Vandenberg, D., 2499
Wisenden, B.D., 2144
Witting, D.A., 2069
Womble, J.N., 1475
Wood, C.M., 618, 942
Wooden, J.L., 2425
Wootton, R.J., 1832
Wright, H.A., 1832
Wroblewski, J., 122, 134
Yan, N.D., 2511
Yaragina, N.A., 1900
Youngson, A.F., 2278
Zemmelink, H.J., 836
Zhang, Z., 2126
Zubchenko, A., 2384
Zuur, A.F., 1918
Zweifel, R.D., 2168

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The index and/or table of contents has been removed and photographed separately within this volume year.

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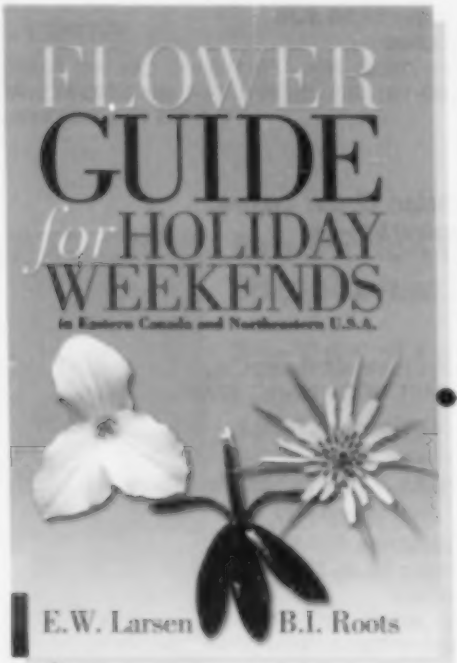

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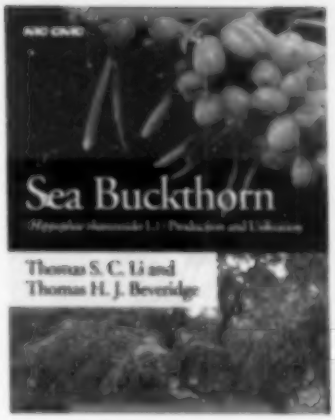

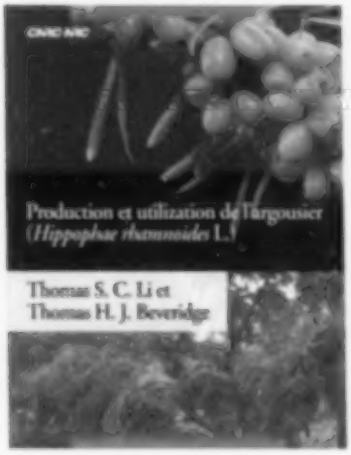

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K. Brander and R. Mohn **2522** Erratum: Effect of the North Atlantic Oscillation on recruitment of Atlantic cod (*Gadus morhua*)

Author Index for Volume 61 AI-1
Contents for Volume 61 C-1

Index des auteurs pour le volume 61 AI-1
Sommaire pour le volume 61 C-1

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Niels G. Andersen and Jorgen Riis-Vestergaard	**2413–2424**	Alternative model structures for bioenergetics budgets of a cruising predatory gadoid: incorporating estimates of food conversion and costs of locomotion
Charles R. Bacon, Peter K. Weber, Kimberly A. Larsen, Reginald Reisenbichler, John A. Fitzpatrick, and Joseph L. Wooden	**2425–2439**	Migration and rearing histories of chinook salmon (*Oncorhynchus tshawytscha*) determined by ion microprobe Sr isotope and Sr/Ca transects of otoliths
Julien M.J. Racca, Irene Gregory-Eaves, Reinhard Pienitz, and Yves T. Prairie	**2440–2454**	Tailoring palaeolimnological diatom-based transfer functions
Carrie A. Holt and Randall M. Peterman	**2455–2470**	Long-term trends in age-specific recruitment of sockeye salmon (*Oncorhynchus nerka*) in a changing environment
Zhenming Su, Randall M. Peterman, and Steven L. Haeseker	**2471–2486**	Spatial hierarchical Bayesian models for stock–recruitment analysis of pink salmon (*Oncorhynchus gorbuscha*)
A. Rindorf and P. Lewy	**2487–2498**	Bias in estimating food consumption of fish by stomach-content analysis
William A. Bennett, Kimy Roinestad, Laura Rogers-Bennett, Les Kaufman, Deb Wilson-Vandenberg, and Burr Heneman	**2499–2510**	Inverse regional responses to climate change and fishing intensity by the recreational rockfish (*Sebastes* spp.) fishery in California
PERSPECTIVE		PERSPECTIVE
L.A. Molot, W. Keller, P.R. Leavitt, R.D. Robarts, M.J. Waiser, M.T. Arts, T.A. Clair, R. Pienitz, N.D. Yan, D.K. McNicol, Y.T. Prairie, P.J. Dillon, M. Macrae, R. Bello, R.N. Nordin, P.J. Curtis, J.P. Smol, and M.S.V. Douglas	**2511–2521**	Risk analysis of dissolved organic matter-mediated ultraviolet B exposure in Canadian inland waters

Continued on facing page / Suite à la page précédente

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The Status of Atlantic Salmon: Populations and Habitats

[Le statut du saumon atlantique: populations et habitats]

	INTRODUCTION	INTRODUCTION
Daniel Boisclair	**2267–2270**	The status of Atlantic salmon (*Salmo salar*): populations and habitats
	ARTICLES	ARTICLES
Michel F. Lapointe, Normand E. Bergeron, F. Bérubé, M.-A. Pouliot, and P. Johnston	**2271–2277**	Interactive effects of substrate sand and silt contents, redd-scale hydraulic gradients, and interstitial velocities on egg-to-emergence survival of Atlantic salmon (*Salmo salar*)
A.F. Youngson, I.A. Malcolm, J.L. Thorley, P.J. Bacon, and C. Soulsby	**2278–2287**	Long-residence groundwater effects on incubating salmonid eggs: low hyporheic oxygen impairs embryo development
Benjamin H. Letcher, Todd Dubreuil, Matthew J. O'Donnell, Mariska Obedzinski, Kitty Griswold, and Keith H. Nislow	**2288–2301**	Long-term consequences of variation in timing and manner of fry introduction on juvenile Atlantic salmon (*Salmo salar*) growth, survival, and life-history expression
Eva C. Enders, Daniel Boisclair, and André G. Roy	**2302–2313**	The costs of habitat utilization of wild, farmed, and domesticated juvenile Atlantic salmon (*Salmo salar*)
Mariska Obedzinski and Benjamin H. Letcher	**2314–2328**	Variation in freshwater growth and development among five New England Atlantic salmon (*Salmo salar*) populations reared in a common environment
Aki Mäki-Petäys, Jaakko Erkinaro, Eero Niemelä, Ari Huusko, and Timo Muotka	**2329–2338**	Spatial distribution of juvenile Atlantic salmon (*Salmo salar*) in a subarctic river: size-specific changes in a strongly seasonal environment
Isabelle L. Girard, James W.A. Grant, and Stefán Ó. Steingrímsson	**2339–2349**	Foraging, growth, and loss rate of young-of-the-year Atlantic salmon (*Salmo salar*) in relation to habitat use in Catamaran Brook, New Brunswick
Donna L. Parrish, Ethan J. Hawes, and Kevin G. Whalen	**2350–2357**	Winter growth and survival of juvenile Atlantic salmon (*Salmo salar*) in experimental raceways
Anders G. Finstad, Ola Ugedal, Torbjørn Forseth, and Tor F. Næsje	**2358–2368**	Energy-related juvenile winter mortality in a northern population of Atlantic salmon (*Salmo salar*)

Continued on inside back cover / Suite au verso

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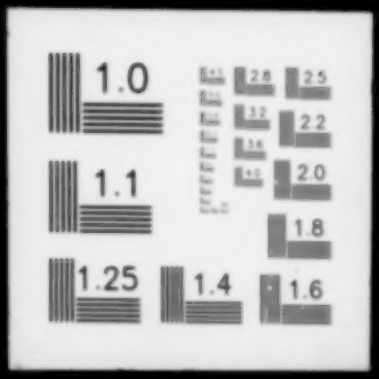
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